MASKING BEHAVIOUR AND RELATED BIOLOGY OF *NOTOMITHRAX URSUS* (OXYRHYNCHA: MAJIDAE)

A THESIS

PRESENTED FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY IN ZOOLOGY

IN THE

UNIVERSITY OF CANTERBURY,

CHRISTCHURCH, NEW ZEALAND

BY

YVONNE MARIANNE PACK

1982

FRONTISPIECE: *Notomithrax* spp. with an adventitious mask of the alga *Halopteris spicigera*.

To

Ivy, David, Albert

TABLE OF CONTENTS

TABLE OF CONTENTS - Cont'd

TABLE OF CONTENTS - Cont'd

LIST OF CONTENTS - Cont'd

TABLE OF CONTENTS - Cont'd

TABLE OF CONTENTS - Cont'd

TABLE OF CONTENTS - Cont'd

LIST OF TABLES

LIST OF TABLES - Cont'd

LIST OF TABLES - Cont'd

LIST OF TABLES - Cont'd

LIST OF TABLES - Cont'd

LIST OF PLATES

LIST OF FIGURES - Cont'd

LIST OF FIGURES - Cont'd

LIST OF FIGURES - Cont'd

ABSTRACT

Notomithrax ursus actively cuts and attaches adventitious materials to the hooked hairs on its dorsal exoskeleton. Investigation of the general biology, ecology, and behaviour of *N. ursus* (Section I) showed that these crabs invest considerable amounts of time and energy, at all stages of their life history, in forming and maintaining the mask. This is consistent with masking being an important adaptation.

Data from the field and laboratory were consistent with the hypothesis that the mask functions to render the crabs eucryptic. *N. ursus* were anachoretic most of the time, remaining closely associated with algal clumps. These crabs were nocturnal and spaced out when active. They exhibited large scale dispersal but movement occurred under cover. In addition, *N. ursus* emphasised behaviours conducive to concealment. When possible, they remained immobile. When active, movement was slow and inconspicuous. Motion was sometimes accompanied by rocking movements. The data indicated that the mask made the crab procryptic not anticryptic. Preliminary experiments suggested that octopuses were important natural predators of *N. ursus*.

Systematic laboratory observations of the interaction between free-ranging *N. ursus* and octopuses demonstrated that the algal mask impaired the triggering of attack by the octopuses in response to distal cues. Experiments with differing backgrounds confirmed that the mask most likely functions as eucrypsis rather than special protective resemblance. In addition, a match between the mask and the background, spacing out between individuals, and immobility of the crabs all enhanced the protection of *N. ursus*.

In an experiment in which *Octopus maorum* was constrained to hunt by visual cues, significantly more unmasked than masked *N. ursus* were attacked in paired presentations against a matching background. Selection indices ranging from 0.63 - 0.76 were calculated. The eucryptic effect of the mask was dependent on ambient light intensity. It is argued that this is a phenomenon of general significance in the evolution of eucrypsis in animals.

CHAPTER 1

GENERAL INTRODUCTION

Majid crabs (Brachyura : Oxyryncha) are an entirely marine group, with a bathymetric range from the intertidal down to over 1,828 m, and are found in all seas except those of the polar regions (Minckiewicz, 1909; Nininger, 1918; Rathbun, 1925; Hartnoll, 1961, 1963; Bruce *et al.*, 1963; Bennett, 1964; Griffin, 1966, 1970, 1973, 1974, 1976; Arnold, 1968; Jones, 1969; Griffin & Tranter, 1974; Haig & Wicksten, 1975). Members of this family usually have long slender legs and elongate chelipeds which, in most cases, are heavier than the ambulatory legs. The carapace is generally elongate-triangular, narrowing in front to a beak-like projection or rostrum which may be entire or bifid; the orbits are incomplete (Plate 1.1). The body surface is generally rough and irregular having tubercules, spines and hairs (Rathbun, 1925; Griffin, 1966; Arnold, 1968).

Over the last decade there have been studies on energy relationships (Aldrich, 1974), the metabolism of napthalene (Corner *et al.*, 1973), respiration (Aldrich, 1975a, b & c; McLeese & Watson, 1968), temperature resistance (McLeese, 1968), isosmotic intracellular regulation (Schoffenields, 1970), micro-spectrophotometry (Hayes & Goldsmith, 1969), eyestalk ablation (Hinsch, 1973), reproductive systems (Hinsch & Cone, 1969; Hinsch & Walker, 1971a, b, 1974), and on the D.N.A. (Vaughn, 1971) of majids.

The last three decades have seen a steady increase in field studies of majid ecology and biology. Aspects investigated include mounding (Baal, 1953; Le Sueur, 1953; Stevcic, 1963), density (Miller, 1975), movement and home range (Hazlett & Rittschot, 1975), migration and geographical distribution (Nishimura & Mizusama, 1969; Roper, 1975), size distribution and sex ratio (Winget *et al.*, 1974), reproductive biology (Stevcic, 1963; Knudsen, 1964a & b; Pereyra, 1966; Hinsch, 1968, 1972; Watson, 1970; Roper, 1975), predatory behaviour (Aldrich, 1976), and agonistic behaviour (Cameron, 1966).

Studies of a more comprehensive nature are scarce. Vernet-Cornubert (1958) studied the general biology of *Pisa tetraodon*. Stevcic (1963, 1967) considered the general biology of *Maja squinado* Herbst. Harntoll considered the biology of the Manx spider crabs (1963) and compared the biologies of British and Jamaican spider crabs (1965). Pereyra (1966) studied the Tanner crab *Chionoectes tanneri* off the Northern Oregon coast. The majority of the Majidae are deep-water animals and this dearth of comprehensive field studies is a reflection of the problems inherent in studying animals from deep water in their natural habitat.

Laboratory studies have been concerned with mating behaviour (Hartnoll, 1968; Berry & Hartnoll, 1970; Savage, 1971; Watson, 1972), larval development (Schelegel, 1911; Lebour, 1927, 1928; Hart, 1960; Hartnoll, 1964; Boschi & Scelzo, 1968; Yang, 1968; Christiansen, 1971; Sandifer & van Engel, 1971; Webber & Wear, 1981), relative growth (Shaw, 1928; Perez, 1929; Teissier, 1933, 1934, 1935, 1955; Vernet-Cornubert, 1957, 1960; Hartnoll, 1974), mounding (Stevcic, 1971), and agonistic behaviour (Hazlett, 1972a, d; Hazlett & Estabrook, 1974).

In New Zealand the family Majidae is represented by 11 genera and 18 species (Griffin, 1966). The sub-family Majinae has three genera, *Notomithrax* (Griffin, 1963), *Leptomithrax* (Miers, 1876), and *Chlorinoides* (Haswell, 1880). At present *Notomithrax* includes five species: *N. spinosus* (Miers, 1876) from Norfolk Island, *N. baeckstroemi* (Balss, 1929) from Juan Fernandez off the coast of Chile, *N. peroni* (H. Milne-Edwards, 1934) from New Zealand and *N. minor* (Filhol, 1885) and *N. ursus* (Herbst, 1788) from New Zealand and South-East Australia. In New Zealand, *N. ursus* is distributed along all the coastline of the North, South and Chatham Islands (Griffin, 1966) and has a bathymetric range from 0 - 73 m.

With the exception of the sub-family Acanthonychinae, which have smooth carapaces (Rathbun, 1925), majid crabs actively select, cut and attach to the hairs on their dorsal surface, materials from the environment (Frontispiece). These materials were termed 'adventitious' by Poulton (1890). Adventitious materials are applied in numerous ways by many animals, utilising a diversity of materials. Although adventitious materials are derived extrinsically, their effect(s) on a perceiver are often the same as materials derived intrinsically. Consequently, the use of adventitious materials has been considered a variation of adaptive colouration and has

been classified accordingly (Poulton, 1890; Cott, 1940; Edmunds, 1974). There are three different categories of adaptive colouration: crypsis, aposematism, and mimicry, differentiated by their effects on the perceiver.

Crypsis is recognised as reducing the contrast between the sender and some part of the environment (Poulton, 1890). Crypsis is further differentiated into procrypsis which is concealment against enemies, and anticrypsis which is concealment against prey (Poulton, 1890; Cott, 1940). Concealment can be achieved by generally harmonising with the environment such that the perceiver fails to distinguish the sender from the background. This phenomenon has been termed 'general protective (or aggressive) resemblance' (Poulton, 1890; Cott, 1940), eucrypsis (Robinson, 1969) or crypsis (Edmunds, 1974). The resemblance of an organism to some object in the environment such that the predator may detect the organism but confuses it with the inedible has been termed 'special protective (or aggressive) resemblance' (Poulton, 1890; Cott, 1940; Robinson, 1969). Edmunds (1974) restricted crypsis purely to general resemblance to the environment, considering special resemblance as a 'Batesian mimicry'. However, as this classification implies that the object mimicked is unpalatable to and not just of no interest to the perceiver, Batesian mimicry may be a misnomer in many cases. Consequently, in this thesis, the categories of crypsis described above will be termed procrypsis, eucrypsis and special protective resemblance, and in reference to prey, anticrypsis.

Aposematism is recognised as enhancing the contrast between the signaller and the environment. In this instance, the perceiver, through prior experience and learning, or an innate avoidance, is warned of an unpleasant or dangerous attribute of the sender. In effect, the signaller is of negative interest to the perceiver.

Mimicry is the resemblance of an organism to an aposematic animal. Batesian mimics are themselves palatable, while Mullerian mimics are unpalatable and derive additional protection by sharing their warning signals with other unpalatable animals. With reference to majids, this use of adventitious materials has been termed masking (Calman, 1911; Flattely & Walton, 1922; Edmunds, 1974), camouflaging (Dell, 1963; Warner, 1977), and decorating (Wicksten, 1978, 1979, 1980). 'Adventitious application' is probably a better term as it does not imply a function for,

Plate 1.1 Unmasked male *Notomithrax ursus*.

Plate 1.2 Masked male *Notomithrax ursus*.

but merely describes the behaviour. However, for reasons of brevity, the term 'masking' will be used throughout this thesis.

The phenomenon of masking among the majids provides an interesting problem to study. The investigation of any biological phenomenon can be considered under four rather distinct aspects: its dynamic control, ontogenetic origins, adaptive significance, and phylogeny (Hailman, 1976).

The investigation of dynamic control involves the questions, how is the character (e.g., mask) constructed and how does the process (e.g., masking behaviour) take place? The dynamic control of masking behaviour has been thoroughly investigated for *N. ursus* by C.L. McLay (unpubl.) who found the same general pattern as reported for *Hyas araneus* (Linnaeus), *H. coarctatus* Leach, *Inachus dorsettensis* (Pennant), *Macropodia rostrata* (Linnaeus), *Eurynome aspera* (Pennant) (Aurivillius, 1889), *Maja verucosa* Milne-Edwards, *M. squinado* (Herbst) (Minkiewicz, 1907, 1909), *Pisa tetraodon* (Pennant) (Milligan, 1915), *Loxorhynchus crispatus* Stimpson and *L. grandis* Stimpson (Wicksten, 1979).

The algal pieces are always applied in the same sequence, the anterior of the body first, starting between the antennae (with the pieces being threaded through the hairs on the rostrum), proceeding to the sides and then the pereiopods (proximal to distal segments, and anterior to posterior pairs). Algal pieces on the anterior of the body are longer than those at the side of the body which are longer than those on the legs and posterior body parts (Plate 1.2). Although the dorsal exoskeleton is covered, the crab continually replaces the pieces previously applied. Materials are secured among the hooked dorsal hairs by a "rubbing" motion. In *Hyas lyratus* Dana (Wicksten, 1976) and *N. ursus* (M. Maryan, pers. comm.) at least, the hooked hairs have rows of microscopic barbs which are presumed to ensure that applied material remains in place.

All the species studied show this general pattern with differences occurring in the manoeuvrability of the chelipeds in transporting the material, the types of masking material used, and whether or not the transplanted organisms are capable of continued growth.

McLay also found that, for *N. ursus*, approximately 20% of the total mask was replenished every 24 hours. The distribution pattern (i.e., the proportion on various body parts) does not change with size and neither

does the number of pieces applied (about 90). However, the average length of each piece increases with increasing size of the crab. Pack (1975) found that algal deprivation resulted in an increase in the total number of pieces of algae applied when *N. ursus* were subsequently exposed to the algae. Algal deprivation also effected a change in the distribution pattern of the algal mask, with the amount on the legs increasing at the expense of that on the body.

The ontogenetic aspect of masking has not been investigated for *N. ursus*. However, while investigating the larval development of Crustacea, Lebour (1927, 1928) noted that masking behaviour was exhibited by majids from the first crab stage onwards. From the brief descriptions provided by Lebour, masking in these young crabs seems identical to that described for older juvenile and adult majids.

The observation of the dynamic control and ontogeny of masking behaviour immediately poses the teleonomical (Mayr, 1961, 1974; Williams, 1966) question, what is the function of this character?

In many spider crabs, body outline and behaviour combine to give the animals the appearance of their habitat. In *Notomithrax* this resemblance has been developed to an unusual extent. The intertidal area inhabited by *Notomithrax* comprises bluish-grey rock and silt covered by a variety of algae, the commonest being the green *Ulva*, pink *Corallina*, and the brownish-yellow *Halopteris*. On casual observation, *N. ursus* appear to favour living amongst and masking with *Halopteris* alga which has a fibrous yellowish-brown holdfast amongst which grit and shell-chips become lodged. To the human eye at least, *N. ursus* closely resembles the background rock, silt and *Halopteris* by virtue of the following features:

(a) the bluish-grey dorsal exoskeleton which blends with the rock and silt;
(b) the presence, over all the exoskeleton, of yellowish hairs which resemble the texture of the algal holdfasts (Plate 1.1);
(c) the presence on the dorsal body exoskeleton of sculptured protuberances which resemble pieces of grit and shell which become entwined in the algal holdfasts;
(d) the presence of adventitious material, including the alga *Halopteris*, on the dorsal surface of the exoskeleton (Plate 1.2).

This similarity between unmasked *Notomithrax* and their background has resulted in the assumption that these crabs are eucryptic, especially to visually-oriented predators (visual crypsis). Similarly, this initial appraisal of the immediately apparent attribute of the algal mask of *N. ursus*, namely that it blends with the crab's background, provides a prima facie case for masking behaviour functioning as visual eucrypsis. Crypsis is commonly thought to result from selection pressures provided by predators (Poulton, 1890; Cott, 1940; Edmunds, 1974) and/or prey (McCulloch, 1925; Edmunds, 1974).

That the mask is simply an example of eucrypsis may have seemed so obvious that it has rarely occurred to researchers that specific evidence would be valuable. There has certainly been a lack of reported laboratory studies on the adaptive functions of this behaviour. For example, of all the previously mentioned studies on the Majidae, only that by Hazlett & Estabrook (1974) provides an hypothesis, with supporting evidence, for the adaptive function of the mask. However, much of the progress made in ethology during the past half decade has been largely due to attempts to obtain evidence pertaining to such seemingly self-evident hypotheses (Tinbergen, 1951; Dingle & Caldwell, 1969; Krebs & Davies, 1981). In this spirit, the aim of this study has been to consider the evidence pertaining to the hypothesis that the algal mask of *N. ursus* functions in crypsis.

Inherent in the hypothesis that the mask is cryptic is the implication that the mask is an adaptation; in the Darwinian sense (Gould & Lewontin, 1979). An adaptation is defined in this thesis as a character that has been shaped by natural selection for a current use (Williams, 1966; Gould & Vrba, 1982) and 'function' refers only to the operation of adaptations (Williams, 1966). Recent workers (especially Gould & Lewontin, 1979) have urged biologists to be more critical in referring to characters of animals as adaptations. Hence, the more basic question of whether masking is an adaptation at all would seem to warrant consideration. As alternative possibilities, masking might have arisen by genetic drift or due to pleiotrophic effects of genes concerned with other characters which have adaptive significance, masking itself being adaptively neutral. Since characters arising in such fashions will not be subject to selection pressures on their own account, and since any system is expected to degenerate to the extent to which there is a relaxation of selection

pressures for its maintenance (Williams, 1966), a measure of the variability of masking within the *N. ursus* population should provide information about whether or not the mask is adaptively neutral. Furthermore, adaptation is generally assumed on the basis of a demonstration of 'functional design' (Williams, 1966), hence one should demonstrate that masking behaviour and the algal mask have the correct qualities to theoretically fulfil a postulated function. Finally, one must not confuse the fact that the character (i.e., the mask) is used in some way, with the primary evolutionary reason for its existence and conformation. The current adaptive utility of masking may be an exaptation (Gould & Vrba, 1982).

Despite the predominance of the hypothesis that the mask functions to conceal the crab from visually oriented predators, many alternative hypotheses are plausible. Eucrypsis need not be visual. Masking materials may disguise the texture (Wicksten, 1980) or emitted chemicals of the crab (personal hypothesis). Among predatory masking crabs, the mask may facilitate prey capture (Stebbing, 1893; Flattely & Walton, 1922; Schmitt, 1968; Wicksten, 1980) by rendering the crab inconspicuous to its prey (anticrypsis). Alternatively, a predator may be capable of detecting the crab but fails to recognise it as something edible, perhaps mistaking it for a clump of algae (special protective resemblance). Many of the sponges and compound ascidians used as masking materials by majids may be noxious or even toxic to the crab's predators (Wicksten, 1975, 1980). Consequently, although the algal mask renders *N. ursus* inconspicuous to humans, it may be chemically aposematic to other predators warning them of its unpleasant attributes. Alternatively, the mask may have a signalling function during intraspecific encounters. Hazlett & Estabrook (1974) hypothesised that the mask may increase a crab's apparent size, increasing the chances of eliciting submissive or flight behaviour in an opponent.

The mask may aid active escape: Milligan (1915) maintained that as the individual pieces of the mask were easily detached they could be autotomised (in the same manner as a limb) when seized by a predator. Wicksten (1980) reported that a masking crab "that is fleeing a predator will often drop off an underwater ledge ... and land on the bottom below". It is possible that the mask aids this escape by stabilising the crab during its descent so that on landing the crab can run off immediately,

rather than having to right itself. The mask may also provide extra drag or hydrodynamic resistance increasing the surface area, thus allowing the crab to drift away rather than plummet straight below the source of danger.

It is possible that the mask has an additional function. Calman (1911) and Milligan (1915) maintained that among the herbivorous species of masking crabs the mask served as a food source. Wicksten (1980) held that although it may now have a cryptic function, masking evolved from feeding behaviour.

Although masking behaviour may have evolved to meet a single selection pressure, it may now subserve several of them.

In essence then, to demonstrate that a character is an adaptation, not an exaptation, and to determine which selection pressures shaped its evolution, one must consider the general biology, ecology and behaviour of the animal in question (Huxley, 1942; Kettlewell, 1959; Tinbergen, 1963, 1965, 1967; Robinson, 1969; Hinde, 1975; Smith, 1977; Clutton-Brock & Harvey, 1979). The results of these studies concerning *N. ursus* and its algal mask are presented in Section I of this thesis.

Having demonstrated a functional design, the next task in any teleonomical study is to explain why the mechanism in question is maintained as a normal characteristic of the species and not allowed to degenerate. If function is to have empirical relevance, it must refer ultimately to the consequences of a difference (Hinde, 1975). Hence, for the hypothesis that the mask functions as visual crypsis, it is necessary to obtain evidence of a correlation between the use of such behaviour and survival against predator pressure. This aspect was pursued in Section II. *Notomithrax ursus* was particularly suitable for this type of study as animals lacking the character under investigation (i.e., the mask) could be obtained without corresponding physiological changes by carefully removing the algae with forceps. In addition, the unmasked state occurred naturally in the field, immediately after moulting.

As 'fitness' (Fisher, 1930) is measured by the number of one's genes represented in the next generation, reproductive success is the ultimate consequence of a function and provides the strongest evidence that a system

is favoured by natural selection (Hinde, 1975). However, a measure of reproductive success requires the monitoring of several generations which, in *N. ursus*, would require at least a 10 - 15 year study. Consequently, reproductive success was not monitored but was inferred from the more immediate consequence of escape by individuals from the predator.

No complete explanation of a biological phenomenon can be achieved without an enquiry into its phylogeny. A study of this type requires data from paleontology, systematics, and biogeography. Although this aspect was not studied for *N. ursus*, Chapter 18 provides a brief review of the studies pertaining to species relationships and a discussion of the possible stages in the evolution of this behaviour.

SECTION I

THE ALGAL MASK AS AN ANTI-PREDATORY ADAPTATION

SECTION I

CHAPTER 2

IS THE ALGAL MASK AN ANTI-PREDATORY ADAPTATION?

In essence, Section I of this thesis was concerned with whether or not masking is indeed an adaptation. To eliminate the possibility that masking behaviour is a pleiotrophic effect it was necessary to determine the occurrence of, and extent of variability of, masking in the population. As the mask appears on an initial appraisal to be an example of crypsis, particularly visual eucrypsis, this section addressed the question, does the mask fulfil the design criteria expected for an adaptation related to crypsis?

Crypsis can be achieved by specialised colouration and/or morphological characters. Animals can possess a general colour resemblance to their background and this can either be fixed (e.g., the stone fish *Synanceja horrida*: McCulloch, 1925) or variable (e.g., octopuses: Moynihan, 1975). Alternatively, they can possess disruptive colouration whereby the body outline is broken up by a combination of colour pattern, or disappearing colouration, where the animals show bright patches when in motion, but suddenly conceal them when resting. Colour can also be utilised to alter the body shading. The shadow of a concealed animal is more noticeable than the animal casting it and dorsoventrally flattened animals can reduce their shadow by squatting close to the substrate. Morphological resemblance can be induced by the development of irregular but bilaterally symmetrical sculpturing of the body surface. Body outline can be disrupted or obscured by the development of thick growths of hair or outgrowths of the body exterior. Finally, crypsis can be achieved by modifying and/or applying the background materials (adventitious application).

If the mask is found to fulfil the criteria for crypsis, one is faced with an interesting phenomenon. The majority of crabs are inconspicuous in form and colour (Warner, 1977) and unmasked *Notomithrax ursus* is no exception. In general, the 'perfection' of an adaptation is believed

correlated with the intensity of selection pressure (Huxley, 1942). Consequently, if the algal mask enables an already inconspicuous or cryptic crab to be more cryptic the selection pressure must indeed be strong.

A defence under some circumstances is very often invalid and occasionally a hindrance or danger under other circumstances. Hence it is advantageous if an animal's total behavioural repertoire is organised to complement the effect of its major defensive system (Cott, 1940; Friedmann, 1944; Robinson, 1969; 1973). Generally, a cryptic animal should remain immobile, at least by day (Cott, 1940; de Ruiter, 1952; Robinson, 1969) and it will be very conspicuous if it rests in the wrong place: it must select a background appropriate to its own colouration and form (Kettlewell, 1955, 1956). In addition, a cryptic animal must adopt a position which provides maximum concealing effect (i.e., it must orient itself correctly with respect to the appropriate background) (Cott, 1940; de Ruiter, 1956). Absolute immobility may be difficult to achieve, so locomotion, when it occurs, must also be inconspicuous. This is often achieved by slowness (Robinson, 1969). Some cryptic insects are known to use dash and freeze movements in which a sudden change from rapid locomotion to immobility may confuse the perceiver. In the case of predation, freezing following locomotion is probably of great importance since movement may have concentrated the attention of the predator on the area in which the insect has come to rest and subsequent movement would be fatal (Robinson, 1969). Movement concealment in some cryptic animals is achieved by a peculiar rocking motion either during, immediately before, or after locomotion (Robinson, 1969). In the case of special resemblance this rocking simulates the movements of plants to wind or water currents (Tinbergen, 1963; MacGinitie & MacGinitie, 1968; Robinson, 1969). Tinbergen *et al.* (1967) and Croze (1970) provided evidence that, in cases where a predator hunts by searching image, it is important for a cryptic species to be disguised at distances greater than the predator could normally detect them. However, the necessity for scattering can be alleviated by polymorphism (i.e., where the population contains several different forms of the one species) (Emlen, 1973; Krebs, 1973). If masking is a mere pleiotrophic by-product one would not expect correlation between masking behaviour and other behaviour patterns of *N. ursus* involved in crypsis. The alternative is to assume that the responsible gene complexes, in addition, just happen to produce these other correlated behaviours. Consequently it was important to determine if *N. ursus* displays other behaviours which, on theoretical grounds, are

supportive of a proposed function for the mask. Hence it was of prime importance to determine when the animal rested and was active, and against which backgrounds, and its orientation with respect to these backgrounds. A knowledge of the modes of locomotion and the dispersal and dispersion of *N. ursus* was also required.

To determine whether the mask was procrypsis or anticrypsis it was necessary to determine when *N. ursus* were exposed to potential predators or prey by studying the diurnal and seasonal activity patterns, dispersal, and geographical distribution of *N. ursus*. In the absence of direct field observation it was necessary to expose *N. ursus* to their feral co-inhabitants in the laboratory.

Adaptations are responses to various selection pressures and heterospecifics provide not only predatory pressure but also competition for resources of food and space, while conspecifics may provide pressures related to reproductive resources (e.g., mates as well as competition for space or shelter). So it was necessary to determine which species co-inhabit the intertidal area with *N. ursus* and with which species these crabs interact. Consequently, it was necessary to determine the life cycle of *N. ursus* as well as its agonistic behaviour.

Finally, it was necessary to examine the data gathered to determine if other functions are feasible in light of the general biology, ecology and behaviour of *N. ursus*.

For investigative purposes the five questions posed have to be answered by way of several different studies concerning the general biology, ecology and behaviour of *N. ursus*.

SECTION I

CHAPTER 3

MATERIALS AND METHODS

Ideally, an investigation of an animal's general biology should include both spatial and seasonal dimensions. However, as only intertidal *Notomithrax ursus* were used in this investigation, the dimension of depth was omitted. The majority of data were collected during a field sampling programme. Where possible, additional data were obtained while collecting and storing specimens for laboratory experiments in this and Section II, and these data corroborated those obtained in the sampling programme and expanded those on copulation and feeding. The additional methods and/or apparatus required in specific studies are described in the appropriate chapters.

3.1 FIELD STUDY

The study site was the Oaro Platform, 24 km south of the Kaikoura Peninsula, New Zealand (43°25'S, 173°42'E) (Fig. 3.1). Although *N. ursus* are abundant all around the Kaikoura Peninsula, Oaro was chosen for study as the beach substratum is comparatively stable (Kirk, 1975) and it suffers the least human disturbance. The platform at Oaro is composed of limestone carved into reefs and channels (Plate 3.1), both of which are covered in algae: mainly *Corallina* spp., *Ulva* spp., *Halopteris* spp. and *Hormosira banski*, with a subtidal fringe of *Durvillea antarctica* and *D. willana* (Plate 3.2). These channels are filled with patches of silt, sand, gravel, stones, and rocks. The sampling area was limited to that which could be *thoroughly* searched during one low tide. Also, it needed to transect an area from the mean high water (MHW) to the mean low water (MLW). The channel chosen fulfilled both these criteria (Plate 3.2).

As spring tides provide the largest areas for collecting, sampling was conducted every spring tide between December 1976 and December 1977, giving a total of 14 samples. The sampling procedure consisted of searching through the algae, mud, and sand, under rocks, stones and in crevices. When an individual was located all relevant data were recorded on a tape recorder and transcribed later. The crab was then replaced. Data were

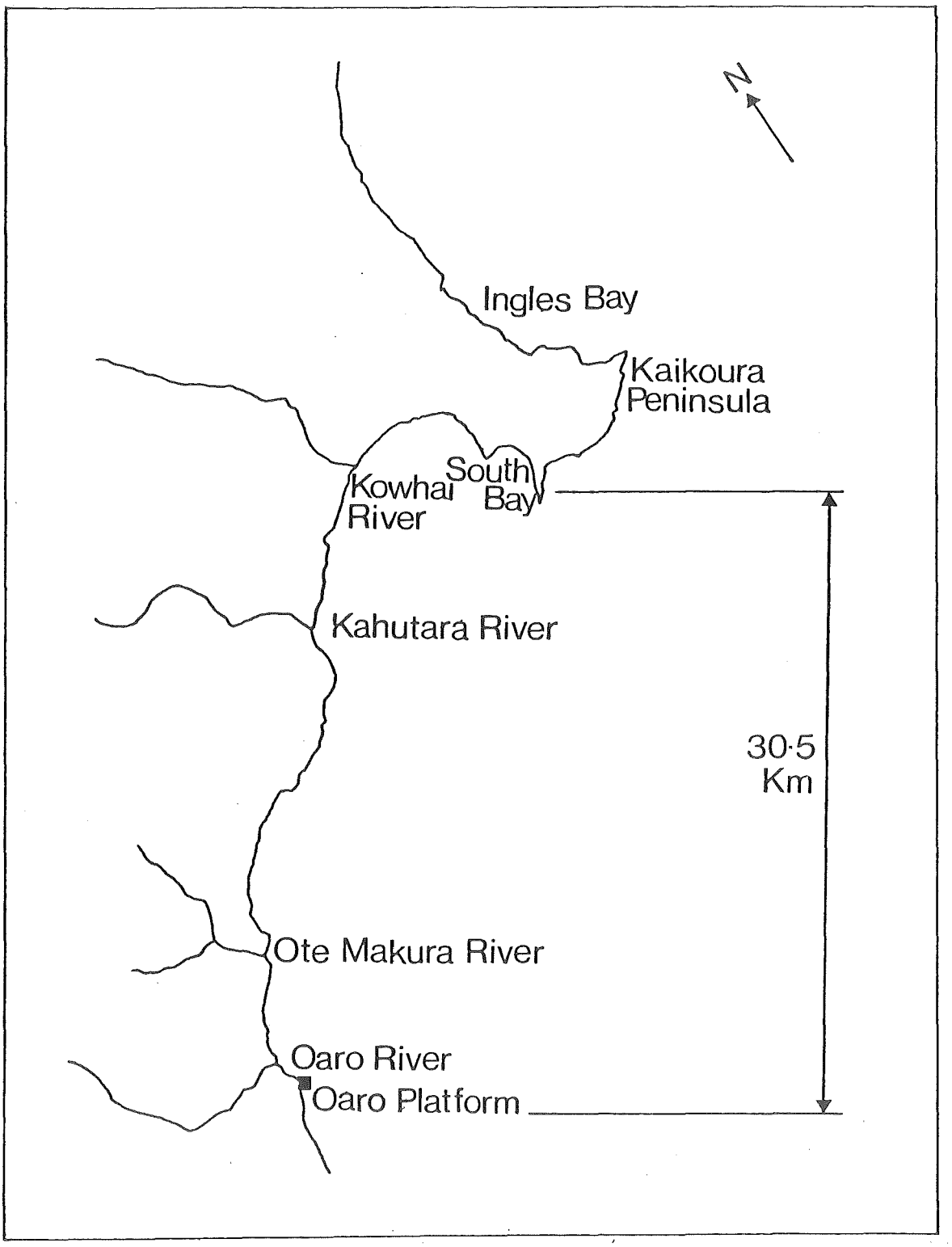


Fig. 3.1 Outline map showing relationship of Oaro Platform to Kaikoura Peninsula.

Plate 3.1 Aerial view of the Oaro Platform (arrow), Kaikoura.
Scale 100 m.

Plate 3.2 Low tide area of Oaro Platform showing the limestone study channel and attendant algae. The photograph was taken midway down the channel; the red bucket marks its beginning.

collected on the species of algae used in the mask, where they were applied and whether they were the same as the background. The sex of the crab, cephalothorax length, maturity and hardness of the exoskeleton were noted, and, where relevant, a sample of the eggs was preserved. The composition of *Notomithrax* aggregations was also recorded. Aggregations were defined as any group of *Notomithrax* found in the same crevice or algal clump or under the same rock or, if not hidden, then within 4 cm (approximately one crab length) of one another. Finally, a record was made of the utilisation of the substrate and the other animals found in the vicinity of *N. ursus*. Any physical abnormalities of individual *N. ursus* were also noted.

Where possible data from the sampling programme were computer analysed using the SPSS package for the Burroughs B618. The remaining data were analysed by hand.

3.2 LABORATORY STUDIES

The bulk of *N. ursus* used for laboratory work were collected from the Oaro Platform, avoiding the channel monitored in the field study. The remainder were collected from various sites around the Kaikoura Peninsula (see Fig. 3.2). Only crabs from the intertidal zone were used.

Crabs were transported in closed plastic bags half full of sea water. These bags were set amidst polystyrene packaging chips and ice in styrofoam boxes. They were then transported either to the Kaikoura field laboratory or direct to the University of Canterbury's marine laboratory. Once in the laboratory the plastic bags were put into holding aquaria and, when the water temperature equilibrated, the crabs were released into the aquaria.

The laboratory at the Edward Percival Field Station, Kaikoura, was mainly used for holding crabs en route to Canterbury. However, some preliminary experiments and observations were conducted there. A continuous supply of salt water was pumped straight from the sea (a distance of approximately 45 m away). The temperature and salinity of this water was the same as that in the crab's natural environment. The aquaria were large and were well lit by natural and fluorescent illumination.

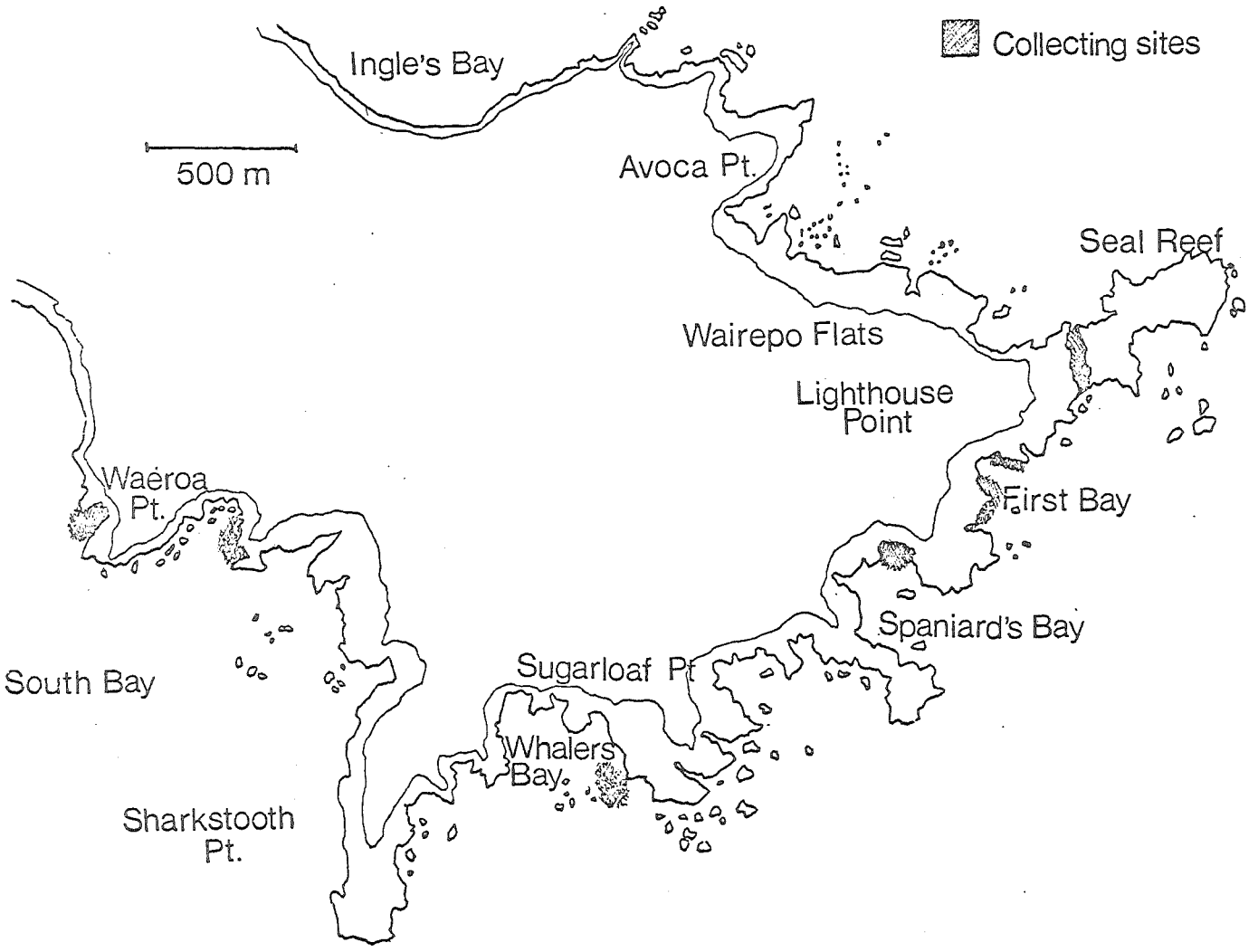


Fig. 3.2 Collecting sites for *Notomithrax ursus* on Kaikoura Peninsula.

In the marine laboratory at the University of Canterbury, Christchurch, the animals were housed and experiments were conducted in a closed circulating sea water system comprised of natural salt water collected from local, pollution-free areas of the sea. Closed systems offer one distinct advantage over open systems: stable and reproducible water conditions. The major disadvantage with a closed system is that it does not reproduce daily and seasonal changes. However, as seasonal effects were monitored in the field study, these factors were of no evident importance. The water was pumped up from a large 'sink' and circulated through all the aquaria. Before being returned to the 'sink' the water was filtered mechanically and exposed to ultra violet light to discourage a build-up of bacterial growth. Water quality was monitored constantly and new salt water was regularly added in small amounts. Only rarely was the total quantity of sea water changed completely. Reserves of sea water were always stored in the dark to prevent decomposition. The average pH of the open sea is 8.3, and the suitable pH range for maintaining marine animals is 7.5 - 8.3 (Spotte, 1970). At Canterbury, the increasing alkalinity caused by evaporation was corrected by the addition of 20 litres of fresh water/day. The salinity of the water was maintained at 36 - 40‰ S. Although the water temperature in the laboratory (17 - 20°C) was, at times, higher than that in their natural habitat, crabs remained alive and healthy for many months. This was expected as McLeese (1968) reported that the majority of spider crabs studied could survive at temperatures well above 20°C. This system fulfilled the criteria, listed by Mariscal (1974), as necessary for maintaining healthy marine animals and was found to be satisfactory for this study.

A 12 hr light : 12 hr dark photoperiod was provided by fluorescent strip lights suspended from the ceiling. Individual tanks were also equipped with a single lamp above them which could be switched on and off when necessary. The aquaria/holding tanks were of three types. Type 1 measured 840 x 400 x 450 cm and had one side made of glass, the remaining sides and floor were concrete. Type 2, 830 x 530 x 550 cm, and type 3, 830 x 830 x 150 cm, tanks had the floor and all sides made of concrete. All tanks were supplied with sea water from the circulating supply. Additional aeration was provided by using a stone bubbler/tank. Several natural rocks were provided as cover for the inhabitants. When housing *N. ursus* the tanks contained clumps of algae, generally *Halopteris spicigera*, but also *Ulva* spp., *Corallina* spp., and some *Laurencia* spp. Crabs were fed on the mussel *Mytilus edulis*.

SECTION I

CHAPTER 4

THE ASSESSMENT OF MATURITY FROM RELATIVE GROWTH

4.1 INTRODUCTION

Behavioural patterns often change markedly throughout an animal's lifetime and the most marked behavioural changes are associated with maturity: this is especially true of breeding and agonistic behaviours. Consequently, it was necessary to be able to differentiate between adult and juvenile *Notomithrax ursus*.

Maturity, in both vertebrates and invertebrates, is accompanied by changes in the rates of differential growth. The study of variables exhibiting differential growth is termed relative growth (Huxley, 1924) or allometry (Gould, 1966). Relative growth rates were obtained using the power function $Y = aX^b$ where Y and X are body variables, b is the regression coefficient (i.e., the rate of change of Y with respect to X) and a is the intercept or size of Y when X = 1 (Huxley, 1924). Such relative growth rates appear as straight lines on double logarithmic plots, with changes in rates, shown by inflexions or discontinuities (Teissier, 1960). Positive allometry occurs if $b > 1$ and negative allometry occurs if $b < 1$. The growth is said to be isometric if $b = 1$.

In decapods, the most striking morphological growth differences are a widening of the abdomen in females and a lengthening and thickening of the chelar propodus in males in relation to the body size. Majid crabs have three identifiable growth stages: immature, prepubescent, and mature (Hartnoll, 1963). These stages are identified by two important points during the growth of the animal (Teissier, 1935): the moult of prepuberty and the puberty moult. At the prepuberty moult the immature proportions of the crab begin their transformation into those of the adult. This point is marked by an inflection in the allometric line and is coincident with the development of the gonads (Aldrich, 1974). Vernet-Cornubert (1958) showed that with *Pisa tetraodon* this inflection appears at varying

individual sizes. At the puberty moult the crab is fully mature and the plot of allometric lines exhibits a discontinuity representing the terminal changes in proportions.

Consequently, an acceptable and quick way to assess the maturity of *N. ursus* was to derive the relative growth graphs for the chelar propodus length and width, and the abdomen width. By means of these allometric graphs the maturity of a crab was determined simply by recording two standard measurements in the field or laboratory on a live crab and determining on which regression line they lay.

4.2 METHODS

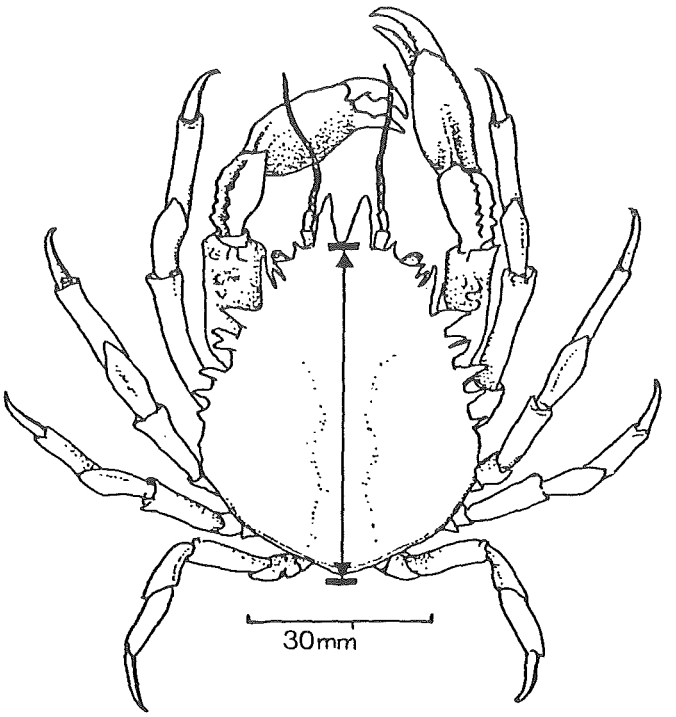
One hundred and five females and 141 males were taken at random from the *N. ursus* populations around the Kaikoura Peninsula and at the Oaro Platform. These crabs ranged in size from 9.5 mm to 46.2 mm in cephalothorax length (CL) and they were collected, transported and housed as outlined in Chapter 3. The defensive behaviours exhibited by *N. ursus* when they are handled (see Chapter 8) prevented the accurate measurement of the chelar propodus and abdomen of live crabs so they were killed and preserved prior to being measured. *N. ursus* were fixated in 5% S.W. formalin for 4 h, washed in tap water for 1 h, and then kept in 70% alcohol + drop of glycerol. Specimens were measured immediately after being fixated to eliminate differences (e.g., shrinkage due to water loss) caused by a prolonged stay in alcohol.

The measurements taken from each crab were the same as those taken by Griffin (1966) and Roper (1975) and are shown in Fig. 4.1:

CL - the length of the cephalothorax was measured along the median line from the posterior margin to a perpendicular connecting the base of the rostral spines. This measurement was taken with the crab ventral side uppermost to avoid the attached algae.

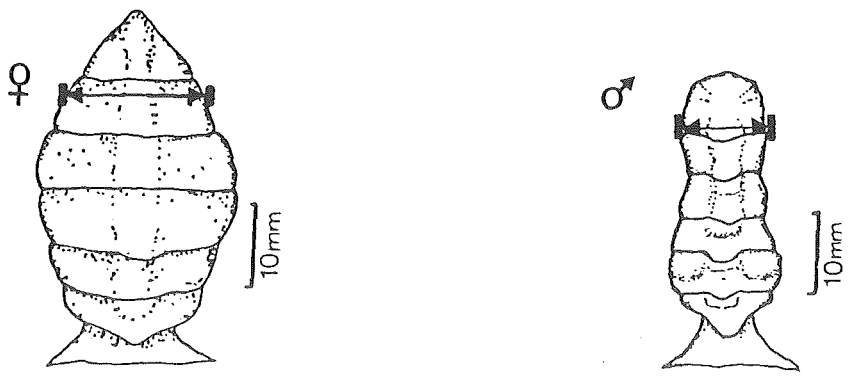
PW - the width of the cheliped propodus, at its widest point.

PL - the length of the cheliped propodus from the ventral junction of the propodus and carpus to a ventral perpendicular connecting the tip of the carpus.



Cephalothorax Length (CL)

Cheliped Propodus Length (PL) & width (PW)



Abdomen width (AW)

Fig. 4.1 Measurements used to analyse relative growth in *Notomithrax ursus*.

AW - the width of the fifth abdominal segment, at its widest point, just below the junction with the sixth segment.

CL and PW were measured *in situ* with Vernier calipers that had an accuracy of ± 0.5 mm. PL and AW were obtained by removing the organs and measuring them with an eye-piece micrometer. To determine the error of measurement, all four measurements were recorded 25 times each from two male *N. ursus* (CL: 25.6 and 13.3). The standard errors and coefficient of variation for each measurement are given in Table 4.1.

Table 4.1 Error of measurement when using Vernier calipers and an eye-piece micrometer with dead *Notomithrax ursus*.

Body Measurement	Standard Error		Coefficient of Variation	
	Crab 1	Crab 2	Crab 1	Crab 2
CL	0.0461	0.4012	0.18	3.024
PW	0.0009	0.0013	0.019	0.063
PL	0.031	0.0018	0.248	0.033
AW	0.0015	0	0.035	0

Sex was determined by the morphology of the abdomen. Among oxyrhynchan females abdomen shape is also sufficiently different to distinguish between immature and mature individuals (Hartnoll, 1968; Hinsch, 1972). The abdomen of an immature female is narrow and does not extend to the base of the legs, while that of a mature female is rounded almost reaching the base of the legs. Maturity in majid females cannot be determined from the condition of the gonads (Hinsch, 1972). Ovulation often occurs a considerable time after mating, hence the ovaries can still be immature at copulation (Hartnoll, 1978). Consequently, a note was made of what shaped abdomen(s) was associated with external eggs. In males, when the testes are ripe, the *vasa differentia* contain a large number of spermatozoa, enclosed in spermatophores, causing these sperm ducts to become swollen and opaque white. Immature ducts are thin and translucent (Hartnoll, 1965, 1968). The gonads of males, whose dimensions fell on the area of overlap of the regression lines, were examined to determine their state of development.

Pre and post-puberty crabs were determined by making scattergrams of the raw data on linear graph paper. Once all the crabs were grouped according to pubescence they were further divided into 2 mm size groups using carapace length, and the arithmetic mean was used to plot the data on log-log graphs which provide the clearest and simplest method for the display of relative growth data (Hartnoll, 1978). Regression lines were calculated by standard regression analysis of the raw data.

4.3 RESULTS AND DISCUSSION

The arithmetically plotted scattergrams of the raw data showed that there are two patterns of growth. The first is seen in those structures which are not sexually important (viz. the male abdomen width and female chelar propodus dimensions). All three measures show a nearly linear rate of increase over the whole range of carapace lengths.

The second growth pattern was apparent in those structures that are sexually important in the adults: viz. the female abdomen width, and male chelar propodus/carapace allometry. The difference between moulting and non-moulting stages was apparent from the discontinuity between the clustered data. Consequently, *N. ursus* could be grouped into mature and prepubescent/immature for the computation of allometric constants. The clustering of data on the graph for females was in agreement with the recognised external abdomen shapes: those with narrow abdomens fell into one group, while those with rounded abdomens were all in the other group. External egg broods were only found on crabs with rounded abdomens confirming that this shape is associated with mature individuals. The large size increase of abdomen width in females is accounted for by the fact that the female abdomen must be wide enough to afford protection to the eggs. In males, those individuals in one cluster had noticeably thicker chelar propodites than those in the other. The male propodus is important for clasping the female during copulation and for displaying during agonistic encounters (see Chapters 6 and 8). Consequently, it increases greatly at the moult of puberty.

As indicated by the scattergrams, there was a considerable range of mature sizes in both males (31.3 - 46.2) and females (23.6 - 40.4 CL).

The difference between immature and prepubescent crabs was less clear. In females neither the scattergram nor a preliminary linear plot of arithmetic means revealed an inflexion in the prepuberty crabs. Consequently, female *N. ursus* may not have a defined prepubescent stage. With the male crabs both the scattergrams and the linear plots of arithmetic means showed a slight inflexion around the 21.0 CL for the PW data and around the 25.0 CL for the PL data. Crabs clustered around the intersecting lines were disregarded and regression lines were computed for immature crabs less than 18.6 CL and greater than 22.0 CL for PW data and for crabs less than 24.0 CL and greater than 27.0 CL for PL data. However, the regression lines for the 'prepubescent' crabs were not statistically different from those of the immature crabs for either the PW or PL variables. In addition, the 'prepubescent' and immature crabs were not distinguishable externally. On the basis of this, and also the arithmetic scattergrams, regression analyses were computed for immature males, mature males, and combined females for PW and PL, and for immature females, mature females, and combined males for AW with respect to CL. The log equations describing these growth relationships are given in Table 4.2, while the graphs are presented in Figs. 4.2 and 4.3.

Table 4.2 Logarithmic equations describing the growth relationships of *Notomithrax ursus*.

Allometric variable	Maturity	Male	Female
Abdomen width	Prepuberty	-	$Y = 0.101\ X^{1.29}$
	Post-puberty	-	$Y = 0.465\ X^{0.997}$
	Combined	$Y = 0.221\ X^{0.9}$	-
Chelar propodus width	Prepuberty	$Y = 0.06\ X^{1.35}$	-
	Post-puberty	$Y = 0.096\ X^{1.33}$	-
	Combined	-	$Y = 0.116\ X^{1.09}$
Chelar propodus length	Prepuberty	$Y = 0.059\ X^{1.36}$	-
	Post-puberty	$Y = 0.195\ X^{1.38}$	-
	Combined	-	$Y = 0.256\ X^{1.19}$

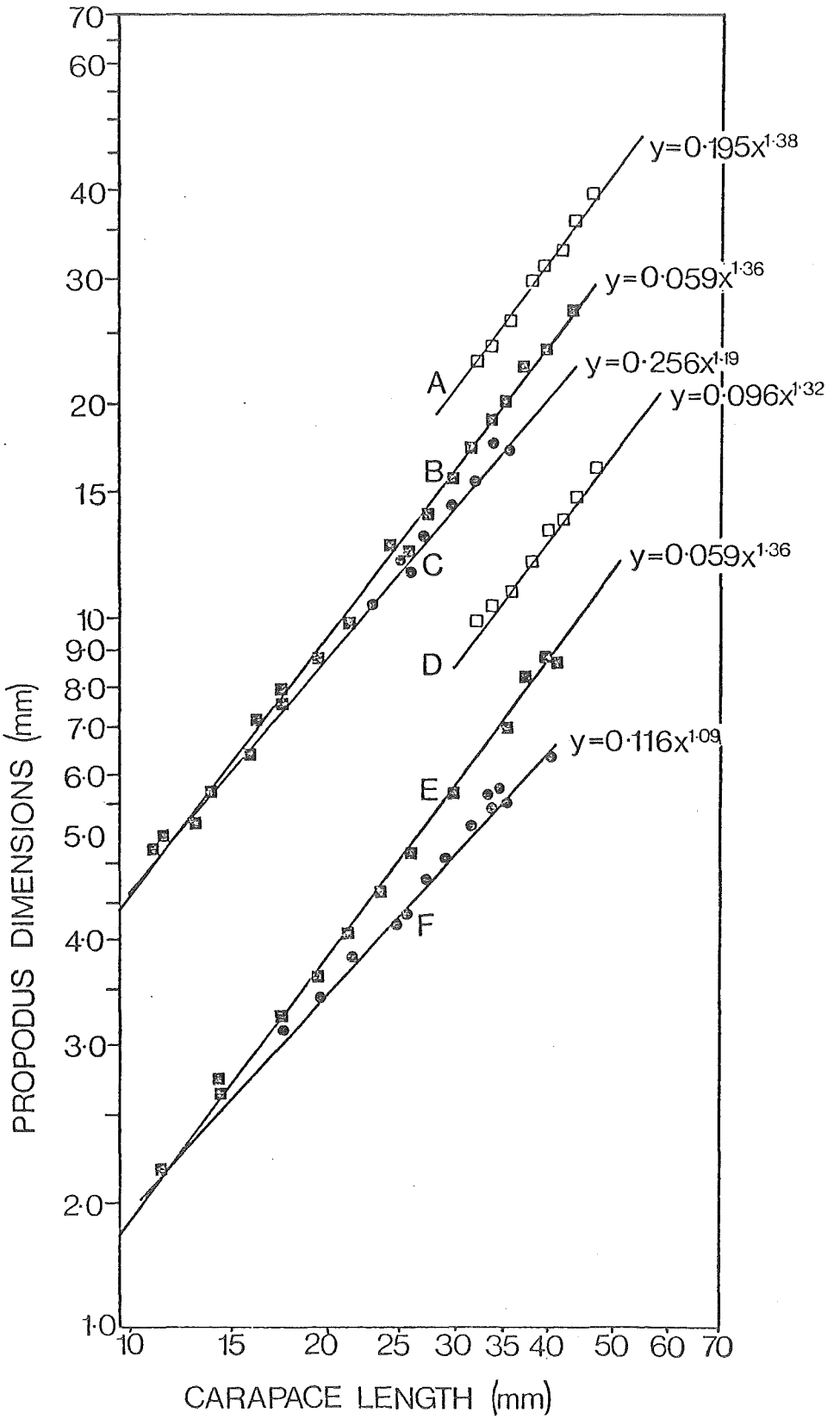


Fig. 4.2 Logarithmic plot of the chela propodus width and length against the carapace length of *Notomithrax ursus*. Propodus length of adult males (A), juvenile males (B), and combined females (C). Propodus width of adult males (D), juvenile males (E) and combined females (F).

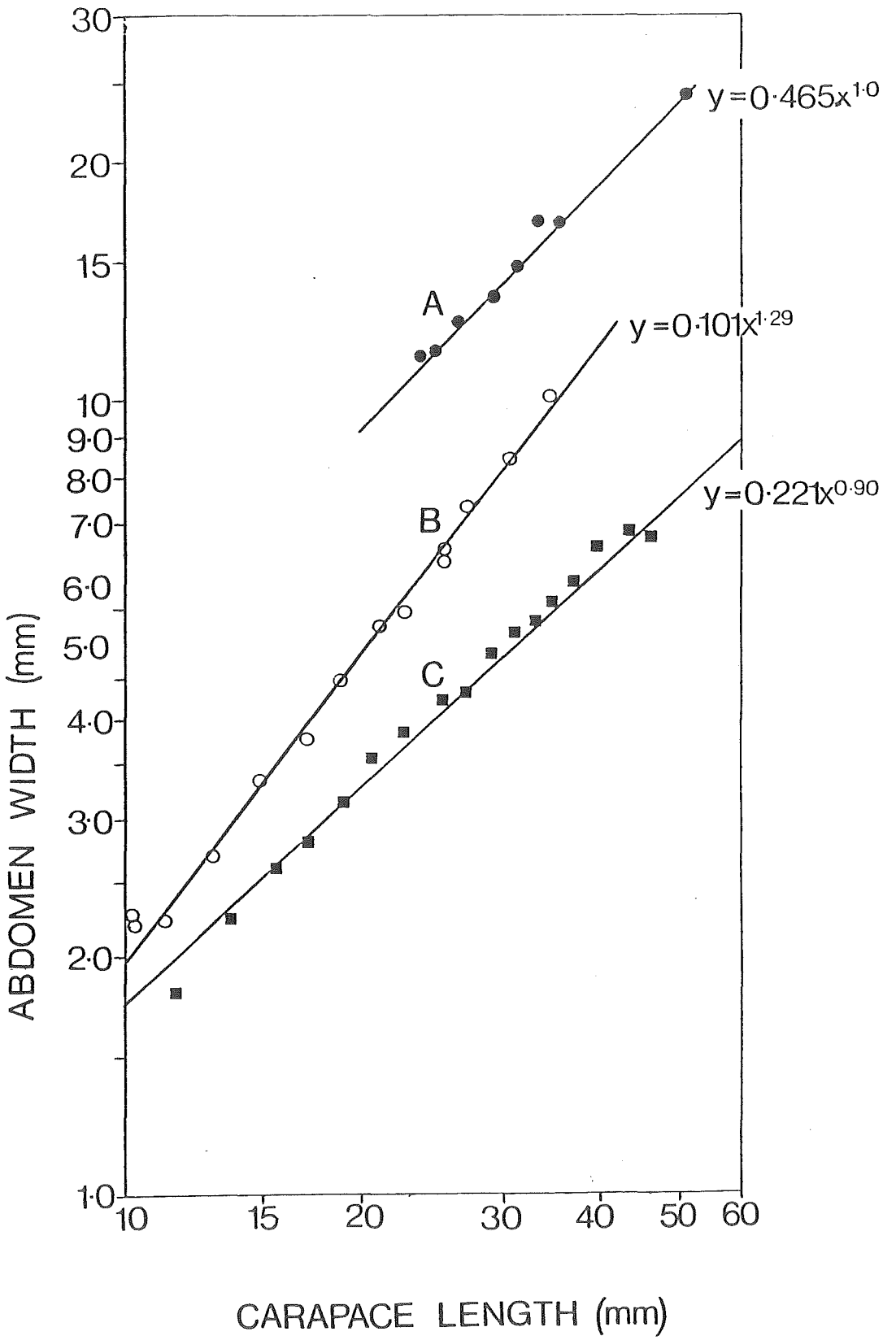


Fig. 4.3 Logarithmic plot of abdomen width against carapace length of *Notomithrax ursus*. A, adult females; B, juvenile females; C, combined males.

These graphs were intended to be used to determine the maturity of the *N. ursus* used in later sections. However, in practice, only the PW/CL graph for males was eventually used for two reasons. Firstly, the maturity of females was immediately apparent from the abdominal shape. Secondly, PW could be measured with calipers so the propodus did not have to be removed.

An examination of males' testes showed that those of the 'prepubescent' crabs were slightly thickened and a milky colour and seemed intermediate between those of the mature and 'immature' crabs. Consequently, in later sections when investigating the possible effects of maturity, crabs which fell on the immature line but which had a CL greater than 22.0 mm were treated separately as 'prepubescent'.

SECTION I

CHAPTER 5

THE OCCURRENCE OF MASKING BEHAVIOUR

5.1 INTRODUCTION

The general sequence and pattern of algal application, replenishment rate, and the effect of algal deprivation on masking behaviour have already been mentioned (Chapter 1). However, to determine the most likely function of the mask it was important to know the frequency of masking and whether the mask was effected by all members of the population or only by certain sex/maturity classes and did the behaviour occur constantly or did it have a seasonal rhythm? Any trends in these types of data would suggest whether the mask was involved in intraspecific behaviours or as a defence against other species or the rigours of the environment.

If the mask has a cryptic or signalling function, some areas may be more important to conceal or highlight than others. Consequently, it was important to know the relative intensity and importance of masking the different body areas. This problem has been partially solved by McLay (pers. comm.) who found that some areas were more likely to be covered than others and that the distribution pattern did not change with size of the individual. However, McLay's study did not provide data from a complete continuous yearly sample from the same population.

If the mask functions as a stabiliser during flight from predators, one would expect that certain algae and certain placement areas would be more efficient than others. Consequently, it was important to determine the type(s) of alga used and its relative placement.

Finally, the algae used in the mask must be related to the background. To function as crypsis the mask should blend with the background, or contrast if it is to be an advertisement. Consequently, it was necessary to determine if *Notomithrax ursus* consistently favoured areas where the mask was the same as, or different from, the surrounding algae.

As arthropods must moult in order to grow, the *N. ursus* population will consist of crabs of two physical states: those whose exoskeleton is hard and those whose exoskeleton is soft. Arthropod muscles require a hardened cuticle to work against; consequently, one would not expect soft crabs to be masked or attempt to mask. Therefore, it was of extreme interest to determine at what stage *N. ursus* were capable of masking. Any masking begun while the cuticle was still soft would suggest that the selection pressure for masking must have been intense for this species to have overcome the difficulties inherent in performing masking manoeuvres against a soft exoskeleton.

5.2 METHODS

Information pertaining to all aspects of the occurrence of masking behaviour was collected monthly, during the field study, in the manner outlined in Chapter 3. The sex of individual *N. ursus* was determined by abdomen shape, while their maturity was determined from the relative growth graphs presented in Chapter 4. Consequently, the population was divided into juvenile and mature females and juvenile, prepubescent, and mature males.

Information regarding the body areas covered and the number of algal species/segment was collated by figuratively dividing the crabs into segments as shown in Fig. 5.1. The leg segments were defined by the natural divisions separating the dactyl, propodus, carpus, merus, and dorsal cephalothorax. The cephalothorax segments were denoted by divisions, based on the following physical characteristics: on B1, B2 and B5 the algae are applied so that the meristems point anteriorly, while on B3 and B4 the algal meristems are directed posteriorly. B1 was defined as that area forward of the side of the chelae, B2 as between that line and the posterior side of the second pair of legs. As the posterior directed algae rarely went beyond the second pair of legs, B5 constituted all the body area posterior to these limbs. As the dactyls, chelae, and antennae bear no algal carrying setae, these segments were not considered. Any missing areas were deleted from the calculations while uncovered areas counted as zero.

As the determination of the types of algae used in the mask was conducted in the field, individual algae were not identified by species,

but just as 'different' from one another. Consequently, although the differentiation of the genera will be accurate, the actual species of, say for example, *Corallina* may have been confused.

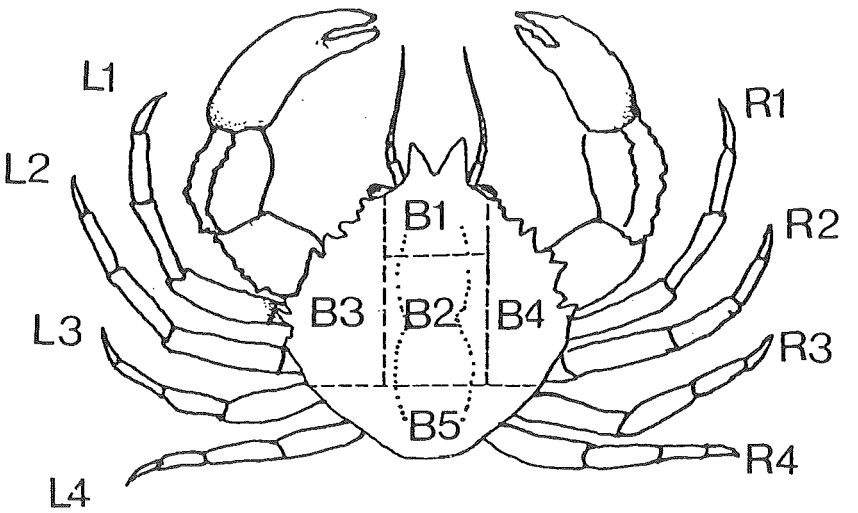


Fig. 5.1 Division of the body of *Notomithrax ursus* for the determination of the areas masked.

At present there are no data concerning how *N. ursus* perceive themselves or each other, nor how they are perceived by other organisms. As the perception of all these other organisms may well differ from our own, the crabs 'match' with the background was determined by classifying the mask according to whether the algae on each segment were the same as or different from the algae (either growing or in the drift-weed) in the area immediately surrounding the crab (i.e., within a radius of one crab length). Where all the algal mask was the same as the surrounding algae it was safe to assume that the mask would 'match' the background in visual, tactile and chemical terms. *N. ursus* were deemed to match (S) the background algae if *all* segments had the same algae as the surroundings and to contrast (D) if none of the segments carried the surrounding algae.

Crabs which contained a mixture of 'matching' and 'contrasting' algae were classified as 'combinations'(C). The mask of these 'combination' crabs could vary from 99% to 1% match with the surrounding algae.

Analysis

Generally, if one leg segment was masked, the others were also masked. Consequently, to simplify the analysis each leg was considered as one segment. Each leg was scored depending on a majority basis. Hence, if two segments were masked and the other not, the leg was classified as masked; and if only one segment was masked, the leg was considered unmasked. As a result, the mask was considered in terms of 13 areas: five body segments and eight legs.

The soft and hard *N. ursus* were analysed separately. Hard crabs were further divided into three categories:

(1) not masked - none of the 13 segments carried any algae;

(2) partially masked - less than seven segments carried any algae;

(3) 'totally' masked - more than seven segments carried any algae.

Seven was used as the deciding criterion between partially and 'totally' masked as generally all segments were masked if the crab had more than seven segments covered.

To the observer, some 'totally' covered crabs appeared sparsely covered even though all segments carried some algae, while others appeared heavily covered. Although these data were qualitative, as well as being analysed with the 'totally' covered group, 'sparsely' and 'heavily' covered crabs were also analysed separately to determine any trends which may have accounted for these differences. Only those crabs which had both chelae intact, and thus had the means to mask fully, were considered in this section.

Where there were sufficient data, all groups were considered in terms of the total sample, sex, maturity, and seasonal differences, and the effect of sex and maturity on the seasonal data. Any damage to the crabs, especially to the chelae, which apply the mask, was noted and considered.

5.3 RESULTS AND DISCUSSION

5.3.1 Hard Crabs

(a) Not masked

Of the 854 crabs sampled only 0.006% (5) carried no algae. All five crabs were large males, two were prepubescent (CL: 33.3, 41.4 mm) and three were adult (CL: 41.6, 41.7, 42.6 mm). All five crabs had both chelae missing, consequently the lack of a mask was in all probability the result of an inability rather than a disinclination to mask. As these crabs were found during April to early July, which is the courtship and copulatory season (see Chapter 6), they may have lost their chelae during agonistic or courtship encounters.

(b) Partially masked

Only 0.03% (23) of the 854 *N. ursus* sampled were partially masked. Of these crabs, 34.78% (8) had an inability to mask as one or both chelae were missing or severely damaged. 53.33% of the remaining 15 crabs were females and another 46.67% were juvenile males. No adult males were partially masked. The majority of the partially masked crabs were found between May and August, the highest concentration being found in June and early July. May to August is the brooding period (see Chapter 6) which may account for the high incidence of partially masked adult females. Presumably the time they spend tending and cleaning the eggs (see Chapter 6) reduces the time available to replenish the mask. The high incidence of partially masked juvenile males seems inexplicable as the puberty moult and copulation occur February - April.

(c) 'Totally' masked

The vast majority of the 854 crabs sampled (96.7%) were 'totally' masked. These crabs ranged in size from 10.1 to 48.0 mm CL.

(i) 'Sparsely' masked. Only 11% (92) of the 826 'totally' masked crabs appeared 'sparsely' covered. The data showed the same trends as that for the partially masked crabs. The majority (56.5%) were adult females, followed by juvenile (17.4%) and prepubescent (12%) males. These crabs were found between April and September with the highest incidence occurring in May and June. Again sparseness of the mask in adult females was in all probability attributable to the time spent tending their eggs.

(ii) 'Heavily' masked. Few (5.6%) of the 826 'totally' masked *N. ursus* appeared 'heavily' masked. Heaviness of masking is clearly related to size: 74% (34) of these crabs were juveniles (50% male and 50% female), 15.2% were adult females, 8.7% were prepubescent males (which are generally larger, especially their chelae, than adult females - see Chapter 4), and only 2.2% were adult males. There was no apparent trend in the months over which heavily masked crabs were encountered. Heavily masked crabs were most frequently found in March (21.7%) then in May (15.2%), late July and December (10.9%), early July (8.7%), April, August and September (6.5%), February (4.3%) and October and November (2.2%). There were no heavily masked crabs found in January. The fact that heaviness of masking was related to size and not sex, maturity, or season, indicates that the mask may be involved in the survival against other species, such as predators, or the rigours of the environment, rather than being involved in intraspecific activities such as courtship.

(iii) Areas covered. The probabilities of specific areas being covered for the total *N. ursus* population and for the different sex and maturity classes are presented in Table 5.1 while the seasonal effects are presented in Table 5.2. The anterior body segment (B1) was always covered, and neither the sex nor maturity of the crab, nor the season, had any effect on this probability. This result indicates that B1 is the most important area of the crab involved in the function of the mask. The areas with the second highest probability of being masked were the legs and, again, the sex and maturity of the crabs had no effect on this probability. There was no difference between the probabilities of the left or right legs, nor first to fourth legs being masked.

A consideration of the remaining body segments revealed some interesting trends. The posterior segment (B5) was rarely covered. It is feasible that this probability was the result of a mechanical inability to reach this segment rather than it not being necessary to mask this segment. This hypothesis is reinforced by the fact that B5 was more often covered in males [who have larger chelae (see Chapter 4)] than in females. The probability that the mid-segment (B2) will be masked was less than that of the lateral segments (B3 and B4) for the whole population. However, juvenile crabs showed no differences in the probability of B2, B3 and B4 being masked, implying that juvenile crabs may have more reliance on being masked than adult crabs.

Table 5.1 The effect of sex and maturity on the probability that a body segment of a hard *Notomithrax ursus* will be masked.

Segment	Total *N. ursus*	Total Females	Total Males	Females		Males		
				Juveniles	Adults	Juveniles	Adolescents	Adults
B1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
R. legs	0.99 - 0.99	0.99 - 1.0	0.98 - 0.99	0.99 - 1.0	0.98 - 0.99	0.99 - 1.0	0.99	0.97 - 1.0
L. legs	0.98 - 0.99	0.97 - 0.99	0.99 - 1.0	0.99 - 1.0	0.94 - 0.97	0.99 - 1.0	0.99 - 1.0	0.97 - 1.0
B4	0.90	0.90	0.89	0.95	0.83	0.89	0.90	0.94
B3	0.88	0.87	0.88	0.94	0.77	0.89	0.88	0.92
B2	0.81	0.84	0.78	0.91	0.74	0.86	0.64	0.57
B5	0.03	0.02	0.04	0.02	0.01	0.04	0.03	0.03

Table 5.2 The effect of season on the probability that a body segment of a hard *Notomithrax ursus* will be masked.

Month	B1	R. legs	L. legs	B4	B3	B2	B5
January	1.0	1.0	1.0	0.92	0.94	0.86	0
February	1.0	1.0	1.0	0.98	0.99	0.93	0.01
March	1.0	0.98 - 1.0	0.99 - 1.0	0.98	0.99	0.89	0.01
April	1.0	0.99	0.97 - 0.99	0.91	0.88	0.83	0.06
May	1.0	0.92 - 1.0	0.99	0.92	0.88	0.86	0.03
June	1.0	0.98 - 1.0	0.98 - 1.0	0.84	0.79	0.67	0.04
July 1	1.0	1.0	0.94 - 1.0	0.84	0.82	0.65	0
July 2	1.0	0.97 - 1.0	0.97 - 1.0	0.71	0.77	0.65	0
August	1.0	0.94 - 1.0	0.94 - 1.0	0.89	0.83	0.56	0.06
September	1.0	0.93 - 1.0	0.93 - 1.0	0.64	0.79	0.79	0.07
October	1.0	1.0	1.0	0.67	0.83	0.83	0
November	1.0	0.92 - 1.0	0.92 - 1.0	0.69	0.77	0.69	0.15
December	1.0	1.0	1.0	0.96	0.91	0.96	0.02

If B5 is ignored, an interesting relationship emerges between the ratio of length of a sharply defined outline of segment to its surface area and the probability that that segment will be masked. In addition, the greater the amount of sharply defined outline the greater the probability the segment will be masked first (see Fig. 5.1). For example, B1 has the greatest ratio of sharply defined outline, having rostral horns, pre-orbital spines, eye-stalks, and anteriorly placed antennae and brightly coloured chelae. The legs have less outline ratio and less probability of being covered than B1, but more outline ratio and more probability than B2 and B3 which have post-orbital spines and two laterally emerging pereiopods. Although B2 has a sculptured surface it has no sharply defined outline, and the least probability of being masked. The fact that more sharply defined segments have a higher probability of being masked perhaps provides an answer to the enigma of why *N. ursus*, which in its natural environment appears cryptic in the unmasked state (see Chapter 1), expends further energy creating a supposedly cryptic mask: the mask may function to obliterate the body outline rather than hiding the animal completely. B1 and the legs are easier for the chelipeds to reach (McLay, pers. comm.) and the fact that evolution has not resulted in chelipeds which can reach areas without a sharply defined outline strengthens the postulate that the mask evolved to obliterate the body outline.

The seasonal data for the total *N. ursus* sample reflected the same trends as shown for the combined year. The order of probability of being masked was B1, then the legs, lateral segments (B3 and B4) and then B2, with B5 being rarely covered. The data on the effect of sex and maturity on the seasonal data showed the same basic trend, although in some months there were insufficient crabs obtained to make a valid comparison.

(iv) Number of algal species/segment. The average number of algal species applied/segment for the total *N. ursus* sample and for the differing sex and maturity classes is presented in Table 5.3, while seasonal differences for the total population are presented in Table 5.4.

There was no difference between the average number of species applied/segment between left and right legs, nor between the legs and B1 for the total population nor for the different sex and maturity classes. However, juvenile crabs applied a greater average number of species/segment to the legs than did the adults. As with the probability of an

Table 5.3 The effect of sex and maturity on the average number of algal species applied to the body segments for the total sample of hard *Notomithrax ursus*.

Segment	Total *N. ursus*	Total Females	Total Males	Females		Males		
				Juvenile	Adult	Juvenile	Adolescent	Adult
R. legs	1.7 - 1.83	1.83 - 1.89	1.64 - 1.77	1.88 - 1.97	1.7	1.64 - 1.85	1.69 - 1.7	1.4
L. legs	1.81 - 1.82	1.84 - 1.86	1.77 - 1.78	1.92 - 1.96	1.7	1.84 - 1.86	1.69 - 1.7	1.3 - 1.4
B1	1.78	1.76	1.8	1.85	1.7	1.89	1.7	1.4
B4	1.6	1.68	1.53	1.9	1.3	1.57	1.5	1.2
B3	1.54	1.67	1.41	1.84	1.4	1.75	1.5	1.2
B2	1.5	1.6	1.44	1.8	1.3	1.63	1.1	0.82
B5	0.05	0.46	0.05	0.04	0.05	0.06	0.05	0.03

Table 5.4 The effect of season on the average number of algal species applied by the total sample of hard *Notomithrax ursus*.

Month	R. legs	L. legs	B1	B4	B3	B2	B5
January	2.6	2.6	2.6	2.4	2.4	2.2	0
February	2.4 - 2.5	2.4	2.4	1.3	2.3	2.1	0.03
March	1.0 - 2.0	1.2 - 2.0	1.2	2.0	1.2	1.8	0.2
April	1.3 - 1.4	1.3 - 1.3	1.3	1.2	1.2	1.1	0.1
May	1.5	1.2 - 1.5	1.5	1.4	1.4	1.4	0.3
June	2.0	1.2 - 1.9	1.9	1.5	1.5	1.3	0.1
July 1	1.6	1.6	1.6	0.8	1.4	1.6	0
July 2	1.9	1.9 - 2.0	1.9	1.3	1.5	1.3	0
August	1.8 - 1.9	1.8 - 1.9	1.8	1.6	1.5	1.0	0.6
September	1.6	1.5 - 1.6	1.6	1.0	1.4	1.4	0.7
October	1.7	2.1	2.1	1.3	1.7	1.7	0
November	1.5 - 1.8	1.5 - 1.8	1.8	1.2	1.4	1.2	0.3
December	2.0	2.0 - 2.1	2.2	2.1	2.0	2.1	0

area being masked, the average number of species applied/segment was greater on the legs and B1 than for the remaining body segments, which again were ranked from B3 and B4 to B2 and B5. This trend is affected both by the sex of the crabs, with males having a greater discrepancy than females, and by maturity, with adults having a greater discrepancy between the number of species applied to B4 - B3. Again this implies that the function of the mask is involved with the size of the crab rather than its maturity.

Seasonally, the total population applied an average of over two algal species/segment during the summer months (December, January, February) and between one and two species/segment for the remainder of the year: implying that the mask is more important during the summer months. The data concerning the effect of sex and maturity on seasonal effects were not sufficient to warrant a comparison.

(v) Number of algal species used. The total number of algal species applied by the total 813 *N. ursus* and by the various sex and maturity classes is presented in Table 5.5, while the seasonal effects on the total population are given in Table 5.6.

The total *N. ursus* sample equally favoured the use of one and two algal species, rarely applied more than three species and never more than six species. There were no differences attributable to sex, but there was a significant difference attributable to maturity with juveniles favouring two species and adults one. The seasonal data indicated that the application of four algal species was related to size: it was most common amongst juvenile females, then juvenile males, then adult females and finally adolescent males.

The seasonal data for the *N. ursus* sampled revealed that one species was favoured during April to September (i.e., during the breeding season) while two and three species were favoured between October and March (i.e., summer season). This favouring of more species over summer is consistent with the data on the areas covered and the average species/segment, and reinforces the implication that the mask is related to size as the majority of the population during October to February consists of smaller juvenile crabs.

Table 5.5 The effect of sex and maturity on the percentage of hard *Notomithrax ursus* which applied a total of 1 - 6 algal species.

No. of species	Total *N. ursus*	Total Females	Total Males	Females		Males		
				Juvenile	Adult	Juvenile	Adolescent	Adult
1	39.6	36	43.1	27.1	50.6	38.8	47.4	65.7
2	39.5	42.5	36.5	49.8	30.5	37.4	36.8	28.6
3	17.5	18.3	16.7	20.3	14.9	19.1	13.7	5.7
4	3.0	27.0	3.4	2.4	3.2	4.7	1.1	-
5	0.2	0.2	0.2	0.4	-	-	1.1	-
6	0.1	0.2	-	-	0.6	-	-	-

Table 5.6 The effect of season on the percentage of hard *Notomithrax ursus* which applied a total of 1 - 6 algal species.

Month	Number of species applied					
	1	2	3	4	5	6
January	10.0	40.0	36.0	12.0	2.0	0
February	7.9	53.8	36.0	3.4	0	0
March	24.2	55.5	18.0	1.6	0	7.8
April	66.2	30.9	2.9	0	0	0
May	59.2	31.1	9.7	0	0	0
June	40.7	34.1	19.8	4.4	0	1.1
July 1	59.2	24.5	12.2	4.1	0	0
July 2	31.2	53.1	12.5	3.1	0	0
August	35.3	41.2	23.5	0	0	0
September	50.0	35.7	14.3	0	0	0
October	33.3	16.7	50.0	0	0	0
November	20.0	53.3	26.7	0	0	0
December	19.6	37.0	26.1	17.4	0	0

Table 5.7 The effect of sex and maturity on the percentage of hard *Notomithrax ursus* which matched their background.

Match with background	Total *N. ursus*	Total Females	Total Males	Females		Males		
				Juvenile	Adult	Juvenile	Adolescent	Adult
Same	71	73	69	76	68	73	60	63
Combination	17	16	19	17	15	19	18	17
Different	12	11	13	7	18	8	22	20

Table 5.8 The effect of season on the percentage of hard *Notomithrax ursus* which matched their background.

Match with background	Jan	Feb	Mar	Apr	May	Jun	Jul 1	Jul 2	Aug	Sep	Oct	Nov	Dec
Same	76	69	62	85	93	40	47	70	88	93	50	100	82
Combination	22	30	23	7	6	32	27	21	6	0	33	0	11
Different	2	5	15	8	0.8	28	27	9	6	7	17	0	7

(vi) Match with background. The data for total *N. ursus* and the various sex and maturity classes are presented in Table 5.7, while the seasonal effects for the total population are given in Table 5.8.

Of the 813 crabs sampled, 72% were totally covered in the same algae as their immediate surroundings. Consequently, 72% can be said to match their background implying that if the mask has a signalling function, it will be of a cryptic or anti-signalling nature. To be advertisement, whether intra or interspecific in nature, the mask would have to contrast with the background. A total of 17.2% partially matched the background and hence were partially inconspicuous. As an advertisement needs to be conspicuous, these crabs can be lumped with the matching crabs. Consequently, only 11.4% did not have the same algae species in the mask as is present in their immediate surroundings. Although I have no knowledge of the perception of *N. ursus*, nor the other species in its habitat, on theoretical grounds a crab covered in a different algal species than its immediate surroundings is less obvious than a crab not covered at all or one that is covered in a non-algal material not normally found in the environment. Consequently, I hypothesise that even the 'contrasting' crabs do not contrast sufficiently for the mask to be an advertisement.

There were no differences between the males and females but mature crabs 'contrasted' with their environment more than the juveniles. Again there was a trend in the size relationship; juvenile females contrasted the least, then juvenile males, adult females, adult males and then, surprisingly, adolescent males.

The seasonal data revealed that the greatest contrast occurred in June and early July and that the incidence of females not matching their background was restricted to the period March to late July (i.e., the brooding season) and December. The incidence of males not matching their background occurred in all months except November, when they were scarce anyway.

5.3.2 Soft Crabs

A total of 23 soft crabs were encountered and the data for the probability that a segment will be covered, the average number of species per segment, the total number of species used and the match with the background are given in Tables 5.9, 5.10, 5.11 and 5.12.

Table 5.9 The effect of sex on the probability that a body segment of a soft *Notomithrax ursus* will be masked.

Segment	Total *N. ursus*	Total Females	Total Males
B1	0.95	0.94	1.00
Right legs	0.78 - 0.95	0.77 - 0.94	0.80 - 1.00
Left legs	0.90 - 0.91	0.88 - 0.94	0.75 - 1.00
B4	0.87	0.83	1.00
B3	0.78	0.77	0.80
B2	0.60	0.61	0.60
B5	0	0	0

Table 5.10 The effect of sex on the average number of algal species/segment applied by soft *Notomithrax ursus*.

Segment	Total *N. ursus*	Total Females	Total Males
B1	1.9	1.8	2.2
Right legs	1.5 - 1.83	1.44 - 1.8	1.6 - 2.2
Left legs	1.7 - 1.8	1.6 - 1.7	1.5 - 2.2
B4	1.6	1.44	2.2
B3	1.4	1.4	1.6
B2	1.3	1.2	1.4
B5	0	0	0

Table 5.11 The effect of sex on the percentage of soft *Notomithrax ursus* which applied a total of 1 - 6 algal species.

Number of species	Total *N. ursus*	Total Females	Total Males
1	30.4	33.3	20.0
2	47.8	50.0	40.0
3	21.7	16.7	40.0
4	-	-	-
5	-	-	-
6	-	-	-

Table 5.12 The effect of sex on the percentage of soft *Notomithrax ursus* which matched their background.

Match with background	Total *N. ursus*	Total Females	Total Males
Same	91.3	94.4	80.0
Combination	8.7	5.6	20.0
Different	-	-	-

Contrary to expectations, all 23 soft crabs had applied some algae to all segments, except B5, suggesting that the selection pressure for masking must have been intense for *N. ursus* to have evolved a mechanism to overcome the difficulties inherent in performing masking manoeuvres against a soft exoskeleton. The probability of each segment of the soft crabs being masked was less than the corresponding segments in hard crabs. However, the probabilities of the various segments being masked had the same ranking as in hard crabs: B1 had the highest probability, then the legs, then B4 and B3, B2, and finally B5.

With the female crabs, the legs had a higher probability of being masked than body areas B4, B3 and B2. This trend was also noticeable for partially masked crabs of both sexes. In all probability, soft and partially masked crabs have not had time to mask completely, indicating one of two things. Either it is more important to mask the legs rather than the body - a trend also shown by crabs which have been algal deprived (Pack, 1975) - or, contrary to McLay's contention, the masking sequence is B1, legs, B2, B3, B4 and B5. As only a few soft crabs were found and only at certain times of the year, there were insufficient data to determine any effects attributable to maturity of the crabs or the season.

Table 5.10 shows that although the average number of species/segment is slightly less in soft crabs, they exhibit the same trends as hard crabs in the order of the number of species applied to the various segments. Males showed a trend towards applying a slightly higher average number of species than females for all body segments. Both males and females favoured the application of two algal species. One species was the next most favoured in the females and the total sample but not in the males who favoured three species next. No more than three species were ever applied by soft crabs, which was contrary to the situation found in hard crabs where the use of four algal species was common and a maximum of six species was applied.

Contrary to the situation in hard crabs, no soft crabs 'contrasted' with the background and only 8% partially matched it. The fact that crabs can mask implies that the muscles can obtain enough traction against the exoskeleton to move, which in turn implies that these crabs are capable of locomotion. Consequently, the fact that 92% of the crabs match their immediate surroundings suggests that gaining a mask has top priority over other behaviours as these crabs mask before moving. There is also a trend for females to be more likely than males to match the

background suggesting that females may need to match more than males. Alternatively, the males may move more than females. On the basis of the data on hard crabs, this is more probably a size-related trend than a sexual one.

SECTION I

CHAPTER 6

LIFE CYCLE OF *NOTOMITHRAX URSUS*

6.1 INTRODUCTION

The period from an organism's conception to the time that it, in turn, reproduces, is known as that animal's life cycle. As an organism's fitness is measured by its contribution to the gene pool of the next generation, it was important to determine if, and how, the mask is related to the life cycle of *Notomithrax ursus*. Life cycles are generally studied with reference to populations, a population being a group of conspecific organisms that occupy a defined area and exhibit reproductive continuity from generation to generation. Populations have several characteristics: e.g., the number of members (abundance), the size of its members (size distribution), and the ratio of males to females (sex ratio). The investigation of the life cycle of a population involves a study of when the young join the population (recruitment), how fast they grow to maturity (moulting), how they mate, reproduce, care for, and release the offspring (breeding). In addition to these time factors, life cycle also involves a spatial component with the differential migration of various sex/age classes throughout the year. In some majids this spatial component involves a bathymetric migration (Allen, 1966).

The most conclusive way to determine the function of a character is to look at its use and to compare the fate of animals possessing that character to differing degrees. All crabs must cast their exoskeleton in order to grow and during moulting the mask is cast along with the exoskeleton. Consequently, newly moulted crabs provide a naturally occurring comparison to masked individuals and, any differences in behaviour of newly moulted crabs or by other species towards these crabs, may suggest the function of the mask.

Post-larval brachyurans have two moults of particular significance: the puberty moult and the terminal anecdysis. The puberty moult is that moult which marks the onset of sexual maturity and this has been discussed

in Chapter 4. In the majids *Maja squinado*, *Pisa tetraodon* (Hartnoll, 1963), *Libinia emarginata* (Hinsch, 1970), *Chionoectes opilio* (Miller, 1975), and *Leptomithrax longipes* (Roper, 1975) the puberty moult and the terminal anecdysis are the same moult and in these species this moult is restricted to a certain time of year. Mating among the Majidae can occur between a mature male and both soft, newly moulted and hardened, mature females. Courtship involves the carrying and guarding of the soft, newly moulted crabs and palpation of the intermoult female by the male (Hartnoll, 1968; Schore, 1968).

The spider crabs *Maja squinado* (Europe) (Stalio, 1877; Stebbing, 1893; Basioli, 1952; Baal, 1953; Le Sueur, 1953; Carlisle, 1957; Stevcic, 1963, 1967, 1971) and *Jacquinotia edwardsii* (New Zealand) (Ritchie, 1970) have been reported to gather in large heaps or 'mounds' at depths of less than 10 m. These mounds have an overall conical shape and are composed of several dozen to several thousands of individuals. Mounding occurred most frequently in association with the period when crabs moulted to puberty and moulting crabs, mainly female, comprised the middle of the heap with males either on the surface of the mound or close by. Mounding in *Maja squinado* has been observed to prevent predation by *Octopus vulgaris* which could not capture the whole mound nor could it extricate individual crabs from the heap (Baal, 1953; Stevcic, 1971). Carlisle (1957) observed that males copulated with the newly moulted females in the mound and hypothesised that the mounds facilitated mating as well as serving to protect those crabs in the centre. Ritchie's (1970) data on *Jacquinotia edwardsii* also suggest that, in addition to protection and mating, some mounds were the result of "certain feeding conditions being satisfied". In view of the facts that *Maja squinado* masks and mounds and that both of these behaviours may be anti-predatory, it would be interesting to note the occurrence of, and construction and composition of, mounds in *N. ursus*.

6.2 METHODS

Information for abundance, sex ratio, size distribution, moulting, and ovigerous females was gained directly from the 870 *N. ursus* sampled during the Oaro field sample. Sampling of the very small *N. ursus* was probably inadequate as these crabs live amongst the tips of the algal fronds. Owing to a malfunction in the tape recorder, one-third of the data obtained for the sample in early July (July 1) was lost. Consequently,

data for early July are presented as that actually recorded and also the predicted values calculated by multiplying the recorded data by 3/2. These extrapolated data are marked by dotted lines on the figures and given in brackets in the text.

Mean sizes given for the total, *N. ursus* and total male and female samples were weighted means calculated by the formula

$$N = \frac{n_1\bar{y}_1 + n_2\bar{y}_2 \ \ldots\ldots\ n_{14}\bar{y}_{14}}{n_1 + n_2 \ \ldots\ldots\ n_{14}}$$

where n = sample size/month and $\bar{y}$ = mean size for that month. Results were graphed and where the lines indicating twice the standard error failed to overlap the results were tested for significant differences using the chi-square test for heterogeneity (contingency tests).

N. ursus pairs of differing sex, size, maturity, and ecdysis state were observed in the laboratory in an effort to determine courtship and copulatory behaviour and mixed groups of crabs in the laboratory were checked for any signs of mounding.

Externally carried eggs were removed from females in the field by prising back the abdomen and carefully picking off a cluster with forceps. These eggs were put into labelled vials with some sea water. Once in the laboratory these eggs were examined under a stereo microscope, their growth stage determined and recorded and then they were preserved in 10% formalin in S.W.

6.3 RESULTS

6.3.1 Abundance

Fig. 6.1 shows that the intertidal *N. ursus* sample had a seasonal fluctuation in abundance: the abundance was lowest in October, rose steadily to peak in April, then underwent a steady decline to September. The data were unlikely to be the result of an aberrant year as the sample had the same abundance for two consecutive Decembers (1976 and 1977) and this seasonal fluctuation was also apparent in the collections of *N. ursus* made in 1975 - 76 and in 1978 - 81.

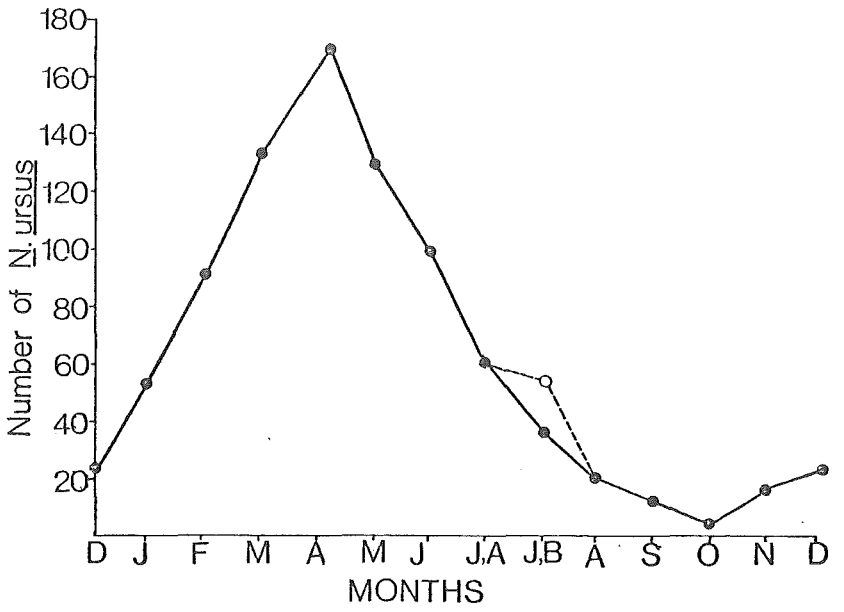


Fig. 6.1 Seasonal changes in the number of *Notomithrax ursus* at Oaro Platform (1976 - 1977). J,A and J,B refer to the 4-weekly samples which both fell in July. Broken line is extrapolated data (see Methods, Chapter 3).

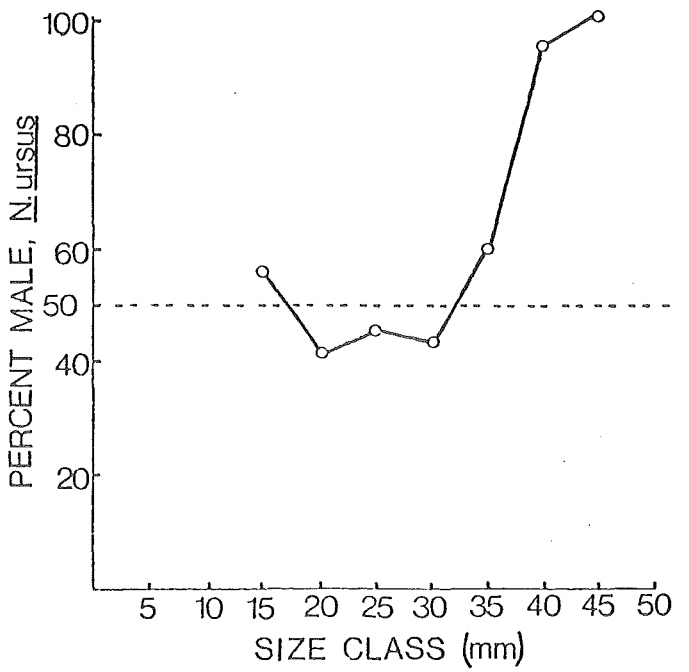


Fig. 6.2 Percentage of male *Notomithrax ursus* for each size class (CL mm).

6.3.2 Sex Ratio

The sex ratio for the *N. ursus* sample was 0.98 males : 1 female. As this differed from Wenner's (1972) finding that it was rare for marine crustaceans to conform to the "normally expected" 1 : 1 ratio, I also calculated the sex ratio using his method. Briefly, Wenner's sex ratio is derived by sorting the animals into discrete size classes and then calculating the sex ratio within each size class. The resultant shape of the graph of the percent of males plotted against size is then compared to the shape of Wenner's four sex ratio graphs. The resultant shape of the graph for *N. ursus* (Fig. 6.2) fits Wenner's 'standard' pattern which is that pattern which emerges from a population with a 1 : 1 sex ratio. The increasing frequency of male crabs greater than 35 mm CL is attributable to the fact that, for males, terminal anecdysis occurred at a larger size than for females. As the smaller crabs were not adequately sampled, one can only assume that their sex ratio (i.e., the primary sex ratio) was 1 : 1.

As the *N. ursus* data gave a 1 : 1 sex ratio when treated by either method, 1 : 1 can be assumed to be an accurate representation of the sex ratio.

The sex ratio was subject to seasonal fluctuations (Fig. 6.3) and fell into four distinct groups. During December to February the average sex ratio was 1.36, while in March to May it was 0.73, June to late July 1.08, and 2.29 from August to November. The latter ratio is probably attributable to the small sample size for this period.

6.3.3 Size (CL mm) Distribution

The total intertidal *N. ursus* sample had a unimodal size distribution, peaking at 25 - 29.99 mm CL (Fig. 6.4). As the distribution was unimodal the mean CL was calculated, being 28 mm. There were no differences in the mean size of males (28.31 mm CL) and females (27.56 mm CL), nor in their size distribution, except that males attained a larger maximum size group (45 - 49.99 mm CL) than females (40 - 44.99 mm CL) (Fig. 6.5).

Seasonally, the size distribution was unimodal (Fig. 6.6). However, the modal group fluctuated in position over the year. The modal group was lowest in November (15 - 19.99 mm CL), increasing to 20 - 24.99 mm in December

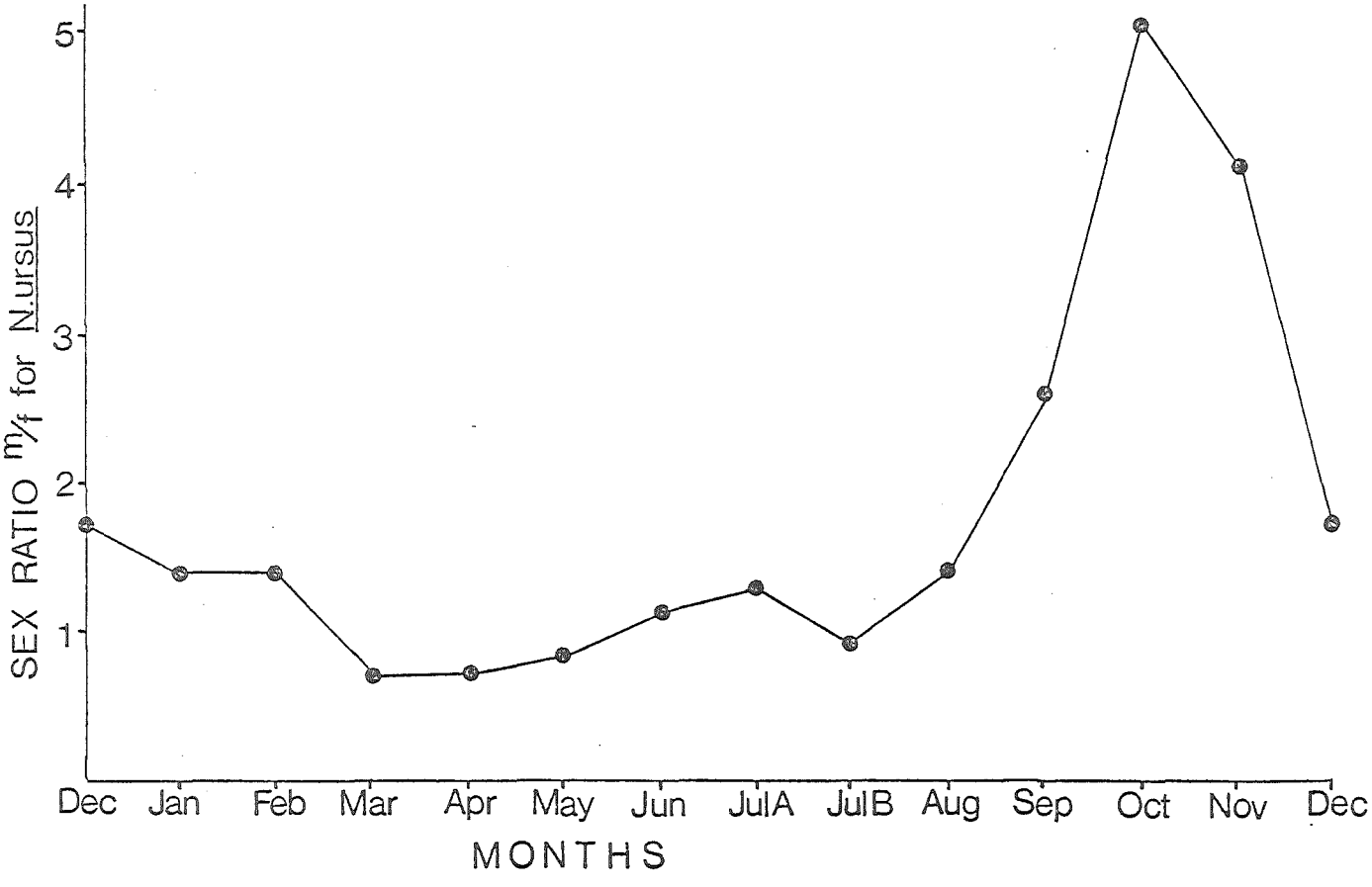


Fig. 6.3 Seasonal changes in sex ratio of *Notomithrax ursus*, Oaro Platform (1976 - 1977). Total sex ratio = 0.98.

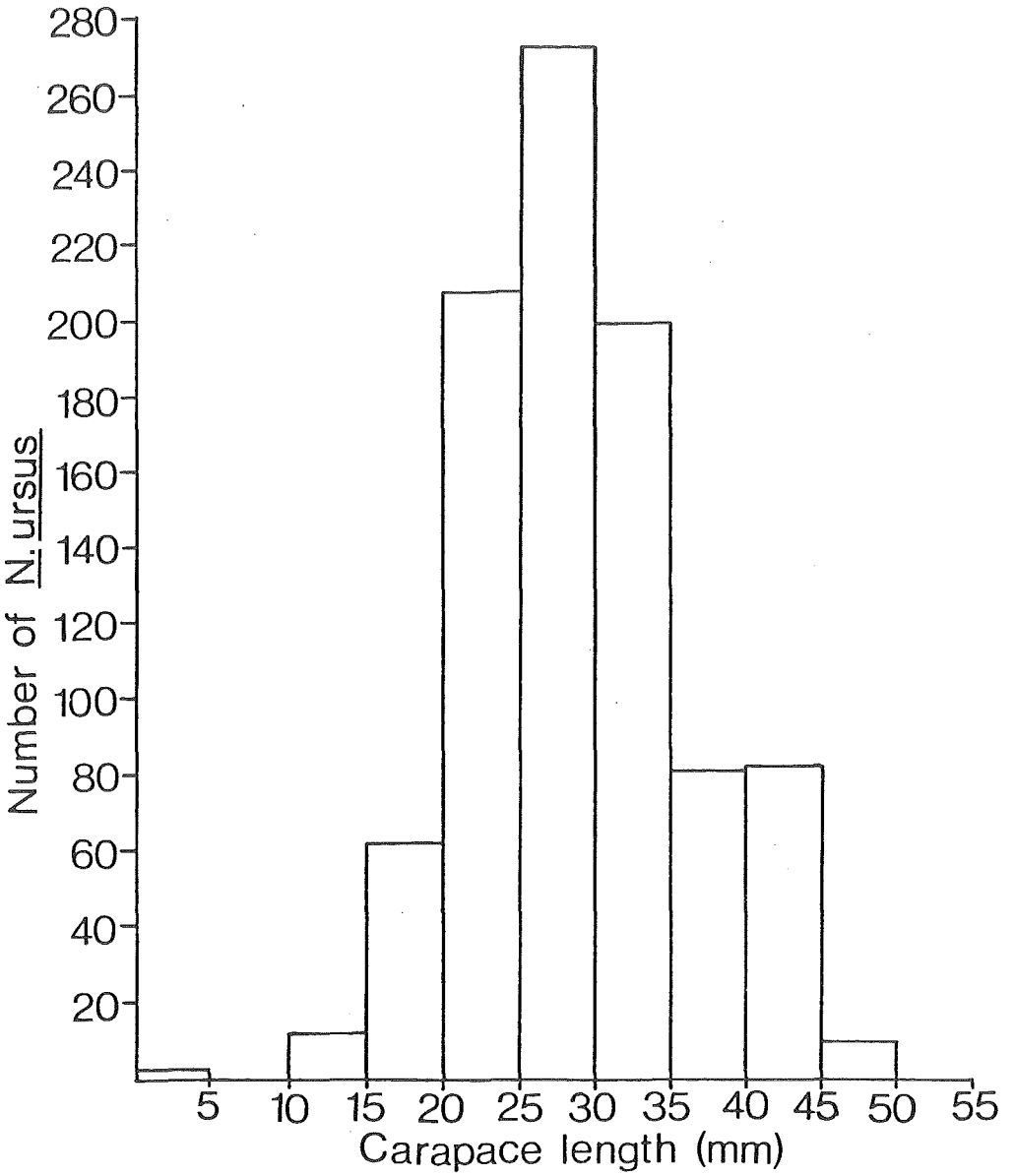


Fig. 6.4 Size-frequency distribution of total *Notomithrax ursus* sample, Oaro Platform (1976 - 1977).

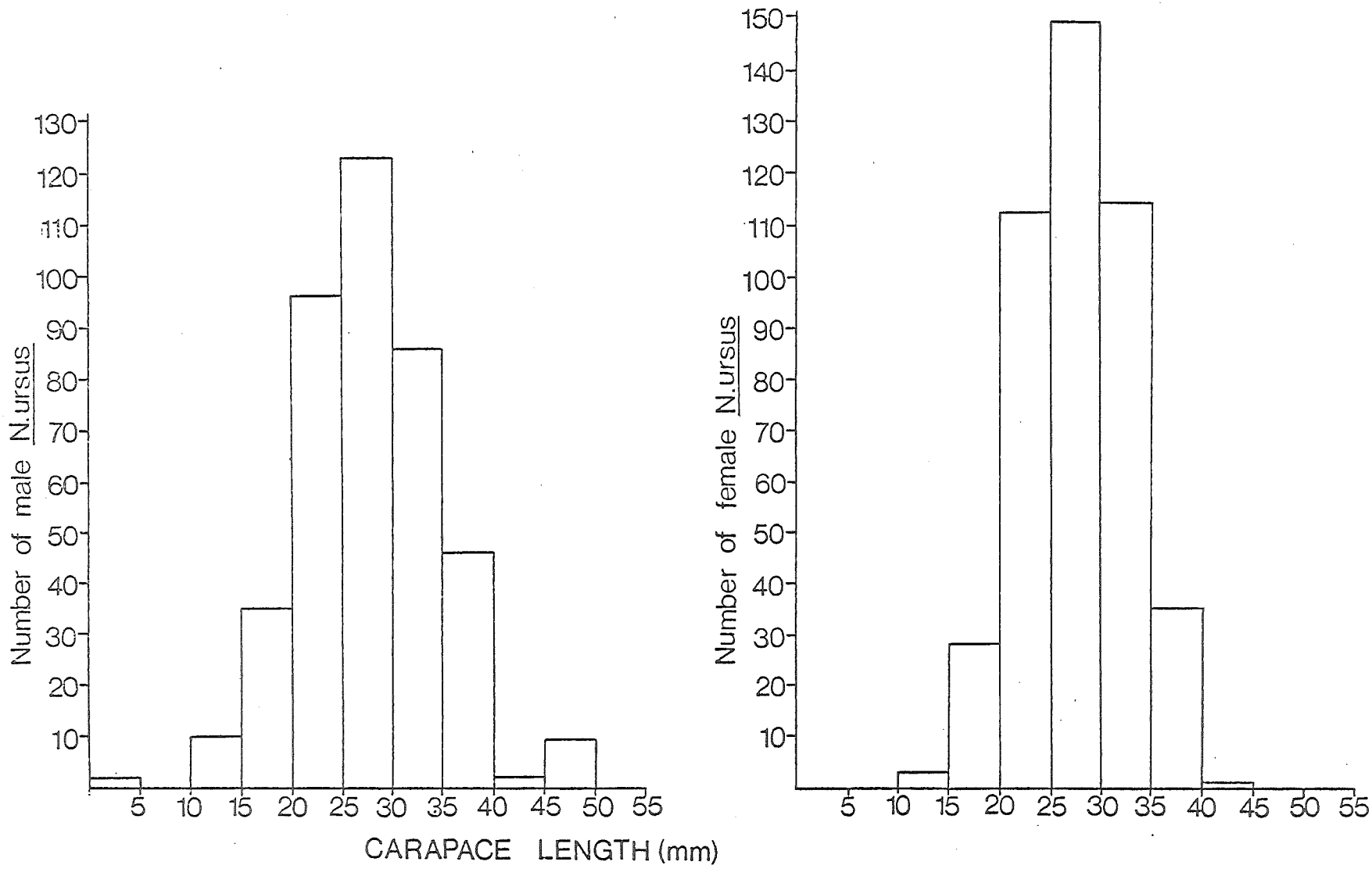


Fig. 6.5 Size-frequency of male and female *Notomithrax ursus*, Oaro Platform (1976 - 1977).

until February, then increasing again to 25 - 29.99 mm in March until April, increasing to 30 - 34.99 mm in May through until August [with the exception of early July where it dropped one group (5 mm)]. In September the modal group dropped 10 mm reverting to the 20 - 24.99 mm size class, before dropping as low as 15 - 19.99 mm in October. These trends are also reflected in the seasonal data for both the male and female samples (Fig. 6.7).

The mean carapace length over the year for the *N. ursus* sample (Fig. 6.8) showed a significant increase between February and March ($t = 3.09$, $p < 0.01$) and a significant decrease between August and September ($t = 2.91$, $p < 0.01$). Males and females had essentially the same pattern except in February when the males were larger ($t = 2.82$, $p < 0.01$) (Fig. 6.9). Large males were present in the sample from December until August. The mean size of males dropped significantly in September ($t = 2.22$, $p < 0.01$), accounting for the drop found in the total sample in September. The mean size of females was lowest in November and increased steadily to February then underwent a significant increase in March ($t = 4.53$, $p < 0.01$) and again in June ($t = 6.19$, $p < 0.01$). The former increase is reflected in the total sample data.

6.3.4 Moulting

During the period December 1976 to December 1980 a total of 46 soft, newly moulted crabs had their measurements recorded (23 from the field study, six during general collections and 17 in the laboratory) although many more were encountered during the whole study (October 1976 - October 1981), mostly during March and April. The data obtained from these recorded crabs are presented in Table 6.1. Soft crabs were only found from September through to May: they were never encountered from June through to August. During the period September to February, the soft crabs were predominantly small males who were moulting from one prepubescent stage to another. The reverse occurred in March to May: the soft crabs were predominantly females and they were moulting from prepubescence to post-pubescence.

6.3.5 Mounding

During the six years spent studying these crabs I observed mounding on only 12 occasions and then never in the field. Table 6.2 shows the conditions under which 'mounds' occurred and the sex, size, moulting state, and masking state of the crabs which comprised them.

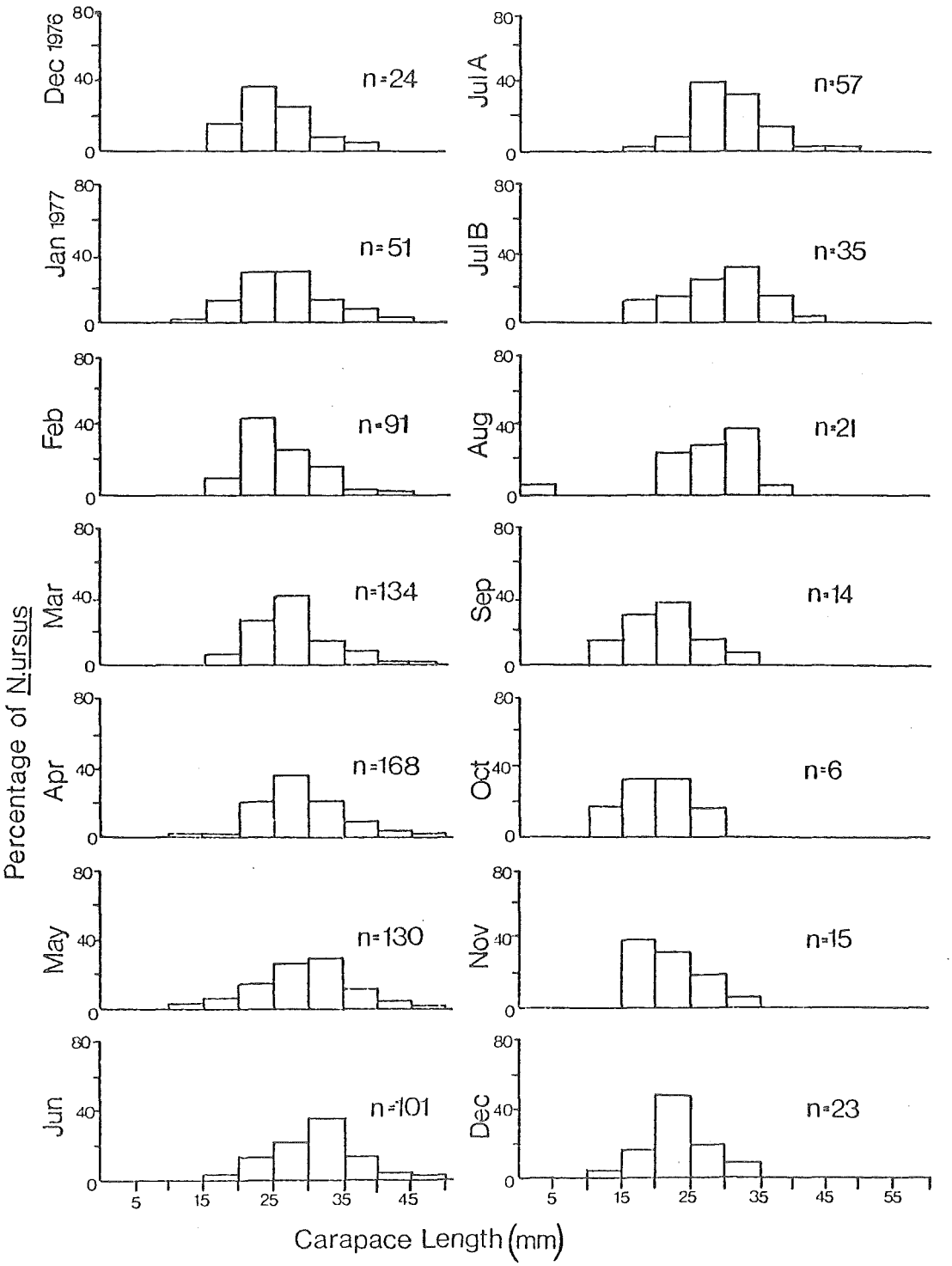


Fig. 6.6 Seasonal changes in size-frequency distribution of *Notomithrax ursus*, Oaro Platform (1976 - 1977).

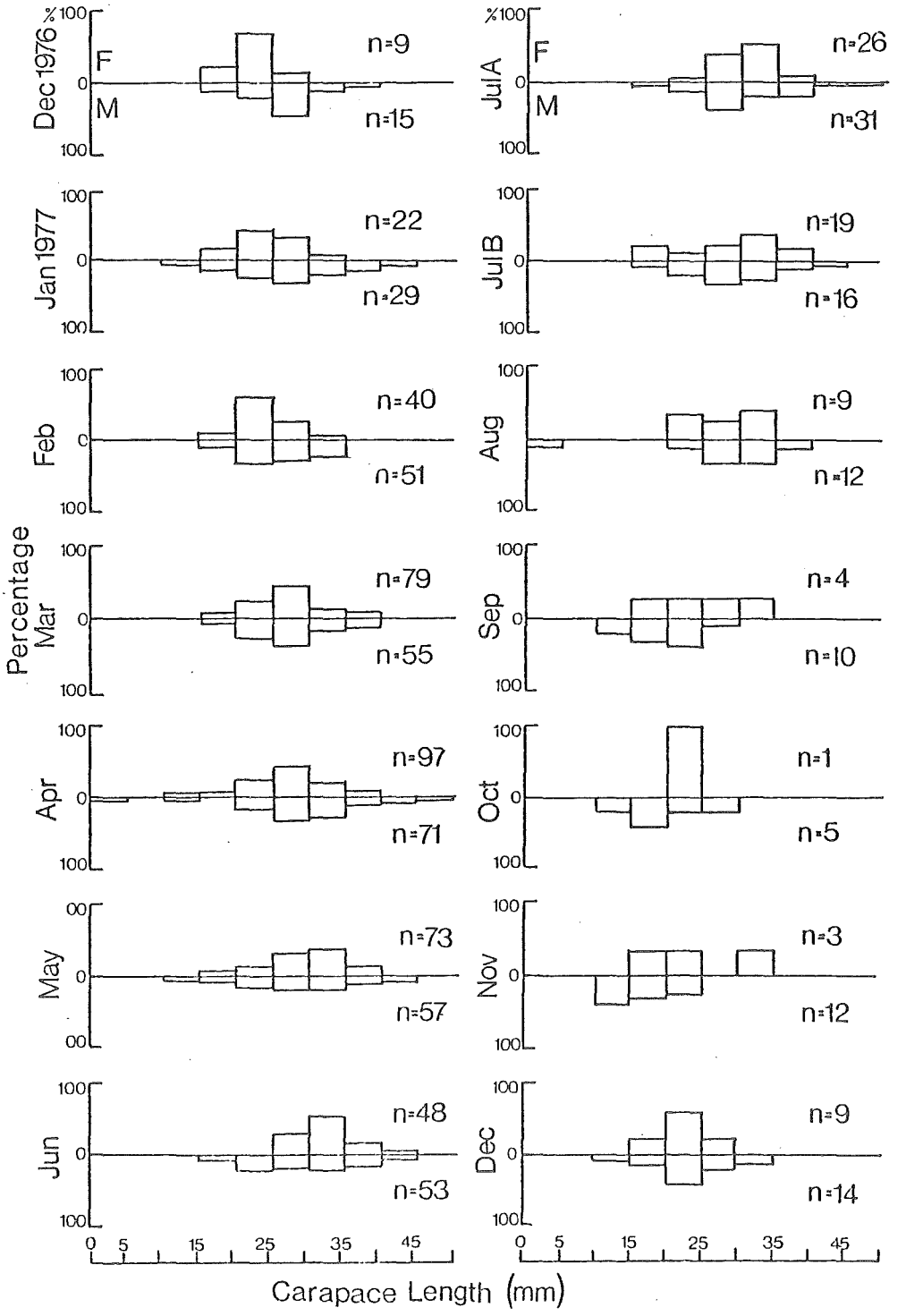


Fig. 6.7 Seasonal changes in size-frequency distribution of male and female *Notomithrax ursus*, Oaro Platform (1976 - 1977).

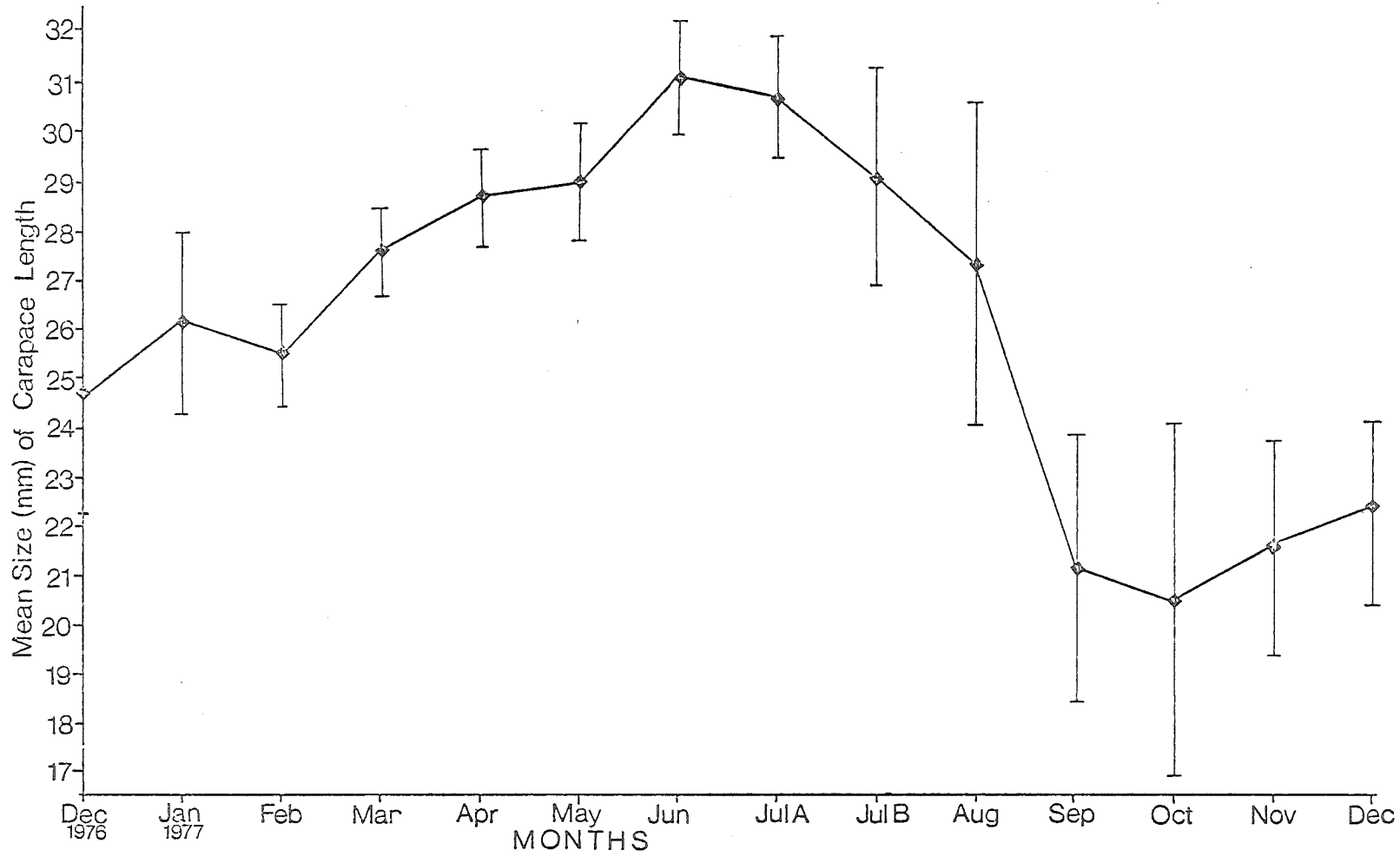


Fig. 6.8 Mean size variation of *Notomithrax ursus*, Oaro Platform (1976 - 1977). Bars are twice standard error.

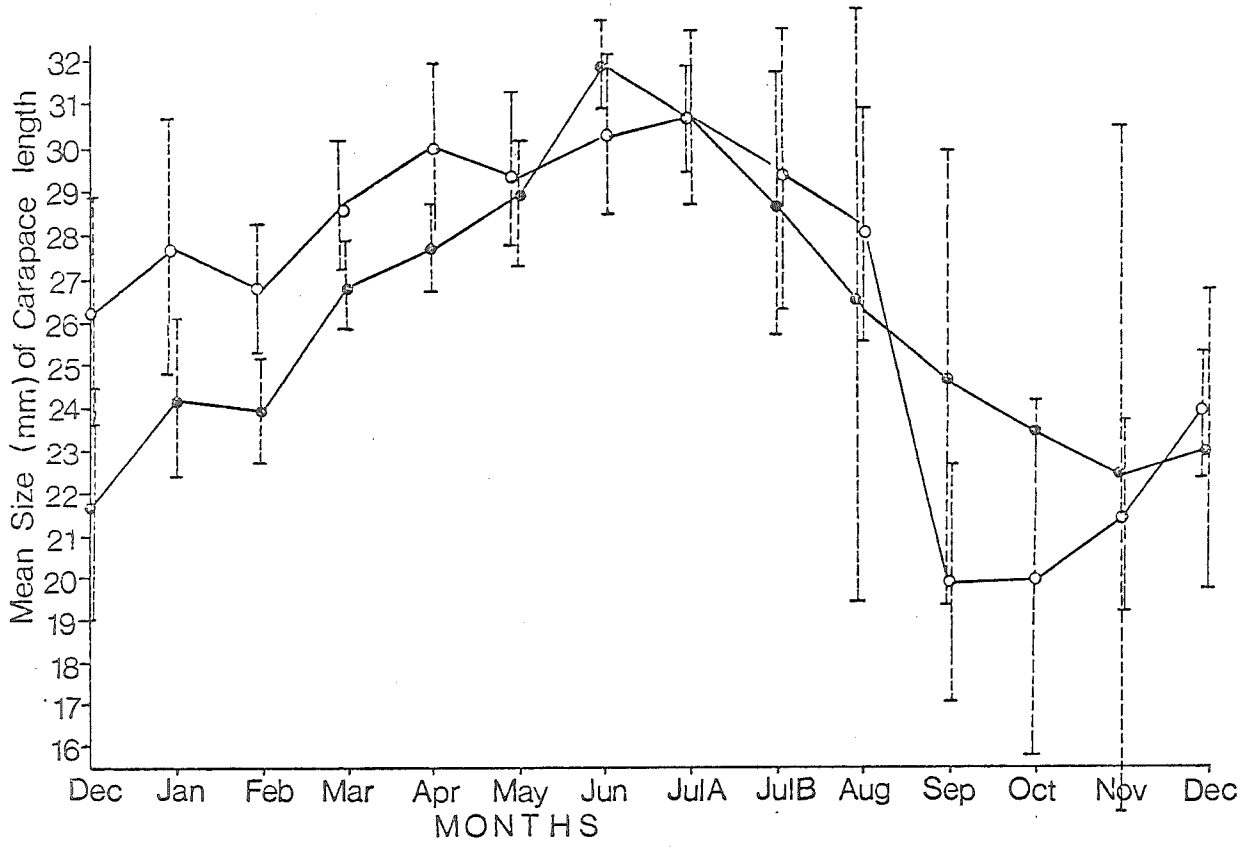


Fig. 6.9 Mean size variation of male and female *Notomithrax ursus*, Oaro Platform (1976 - 1977). Open circles, male; closed circles, females. Bars are twixe standard error.

Table 6.1 The seasonal occurrence, sex, and maturity of newly moulted (soft) *Notomithrax ursus* encountered December 1976 - December 1980.

Month	Total *N. ursus*	Sex		Prepubescent to: Prepubescent		Post-pubescent	
		M	F	M	F	M	F
Sep.	2	2	0	2			
Oct.	4	4	0	4			
Nov.	4	3	1	2		1	1
Dec.	5	4	1	3	1	1	
Jan.	4	2	2	2	2		
Feb.	1	1		1			
Mar.	4	1	3		1	1	2
Apr.	19	5	14	5			14
May	3	0	3				3
Total	46						

Mounding occurred in the presence of algal cover only once and in the presence of a particle substratum on only two occasions. However, mounding could not automatically be induced by depriving the crabs of algae. On nine occasions, mounding crabs were exposed to a predatory octopus while, on a further two occasions, they had been subject to human interference (stimulation by glass rods and cotton swabs).

Although the mounds occurred concurrently with the moulting period (September - May) they were never comprised of newly moulted soft crabs. Even when many crabs were present, the mound never contained more than five crabs and there was no order to the sex, size, or possession of a mask, nor distribution of the constituent crabs (Plate 6.1).

6.3.6 Breeding

(a) Courtship

No precopulatory (i.e., courtship) behaviour was observed in the field and only one instance of courtship behaviour was observed in the

Plate 6.1 Mounding behaviour exhibited by unmasked *Notomithrax ursus*.

Table 6.2 The conditions under which 'mounds' occurred and the sex, size, and moulting state of *Notomithrax ursus* which comprised them.

Date	Number		Masked		Unmasked		Size Range	Moulted	Conditions			Predator
	Mound	Possible	M	F	M	F	(CL mm)	(Soft)	Lab.	Algae	Particle Substrate	Present
1/12/74	5	15	-	-	3	2	22.0 - 32	-	✓	-	✓	- **
16/11/77	5	6	1	5	-	-	14.2 - 31.5	-	✓	-	-	'Human' *
30/11/77	3	7	2	1	-	-	15.4 - 26.3	-	✓	-	-	'Human' *
30/12/77	4	8	2	2	-	-	27.3 - 40.0	-	✓	-	-	*Octopus*
11/ 1/78	3	8	1	-	2	-	27.0 - 33.8	-	✓	-	-	*Octopus*
17/ 1/78	3	6	-	-	-	3	26.9 - 32.7	-	✓	-	-	*Octopus*
21/ 1/78	2	6	-	-	2	-	28.5 - 32.9	-	✓	-	-	*Robsonella*
22/ 3/78	3	6	-	-	-	3	21.7 - 22.7	-	✓	-	-	*Octopus*
3/ 6/78	4	4	2	-	-	2	29.0 - 31.6	-	✓	-	-	*Octopus*
19/ 9/78	2	2	1	-	1	-	22.2 - 22.5	-	✓	-	-	*Octopus*
27/12/78	2	2	1	-	-	1	27.4 - 29.0	-	✓	-	-	*Octopus*
8/ 5/79	2	2	-	1	-	1	34.5 - 35.5	-	✓	✓	✓	*Octopus*

* Crabs were being stimulated by glass rod and cotton swab and were also subject to handling.

** Crabs had been deprived of algae for seven days (Pack, 1975).

laboratory. This courtship involved an unmasked, soft adult male and a moderately masked, intermoult female carrying late stage eggs and took place in a small observation aquarium (15 x 32 x 15 cm) also containing a non-ovigerous mature female, an immature female, an adolescent male, and two immature males. Observation was made in the dark with a 'safe-light' on and the crabs had been in the aquarium for 2 h prior to the encounter. The male sat on top of the female and disembarked when a juvenile male backed into the pair. The male then moved briefly under the female, dorsum to her ventrum, retreating when the other occupants began to move around the tank. After departure of the soft male, the ovigerous female began to aerate her egg mass (see Chapter 8). Later, the ovigerous female was resting, her chelae tucked back under her body. The soft male moved up to the female and twice attempted to sit on her back, and was tipped off twice. The male then moved under the female, abdomen to abdomen, and clasped her abdomen with his chelae. The male was unable to wriggle right under the female's abdomen which was distended with eggs. He then pulled himself out from under the female and, grasping a clump of hairs and associated algae on her rostral area in his chela, attempted to pull himself on to the female's back again. But the female resisted by arching backwards, flailing the first and second pairs of legs, throwing the chelipeds back and apart, effectively 'elbowing' the male with the joint between the propodus and carpus and actually pinching him when she could reach. The male began to grip and release the hairs/algae on her rostral area with the dactyls of his chelipeds. Meanwhile, the female continued to struggle and throw her chelae up and out. This cycle of the male continually grasping/releasing hair/algal clumps while the female resisted, continued for over 30 minutes. During this time the male made contact with hair/algal clumps in the rostral and branchial regions, and her first pereiopods. The male attempted to block the action of her chelae by pushing his spare chela against them. At one stage the female also began to aerate the eggs with one chela while resisting the male with the other. Eventually the male released his grip and was tipped off the female who raised herself up and arched backwards. The male then went to another part of the aquarium and remained there for the remaining half hour of observation.

On one occasion, three intermoult adult males briefly flapped their abdomens rapidly and repeatedly when an intermoult adult female was initially introduced into their aquaria, then refrained from any further behaviour towards the female during the following 2 h of observation.

(b) Copulation

Various stages of copulation were observed in the laboratory with four heterosexual pairs of crabs in which all the females had a hardened exoskeleton. An attempted homosexual copulation was also observed between a male pair, both crabs having hardened exoskeletons. The copulatory sequence described below is derived from the observations (at various, but overlapping stages) of conjugation in the four heterosexual pairs:

The male approached the female, rostrum to rostrum. He gripped the female's dorsum with his most anterior two pairs of legs, the foremost pair in the vicinity of her eyes. The hinder two pairs of legs were used to balance the male on the substrate. The male then manipulated the female with his chelae, making several attempts to turn the initially resistant female so that they were sternum to sternum. When this position was achieved the male rocked backward so that the female-over-male position was achieved. When in this position the male held the female with his chelipeds, which were folded over her carapace. His legs were also interlaced between her legs and folded over her carapace. It appeared as if most of the ambulatory legs of the female were used for supporting the pair and for locomotion. The female lowered her abdomen and the male inserted his abdomen inside the female's. This resulted in his pleopods being directed towards the female's body. I was unable to ascertain if the pleopods were actually inserted into the female's vulvae.

The male crabs ranged in carapace length from 29.0 to 46.7 mm and had the secondary sexual characteristics of an enlarged propodus and, in three of the four, a notched dactyl. Females ranged in carapace length from 25.6 to 40.4 mm and all had the rounded abdomens and plumose pleopods. Both females examined in detail had large visible vulvae. When the allometric variables for these copulatory crabs were plotted on the relative growth graphs (see Chapter 4) they lay on the uppermost lines, confirming that the discontinuity in the regression lines signifies the puberty moult in *N. ursus*.

The vulvae of prepuberty moult females were not large enough to accommodate the pleopods removed from these sexually mature males, corroborating Hartnoll's (1968) claim that in the Majidae the vulvae only become large enough to permit mating at the puberty moult.

Only one of the four females had eggs externally at the time of copulation and, contrary to Hinsch (1968) and Knudsen (1964b), these eggs were at the early (Stage 1), not pre-hatch (Stage 4) stage of development.

One of the females spawned within 24 hr of copulating; thus she must have had ripe eggs in the ovaries.

The algal mask had no evident importance in copulation. In the one homosexual and two heterosexual pairs both partners were sparsely masked (seven segments covered, see Chapter 5), in the third male-female pair both were moderately (all segments) covered and, in the final pair, the male was moderately masked while the female was heavily masked. There was no pattern to the areas of the body covered nor in the type and amount of material applied.

(c) Brooding

The field study and general collections showed ovigerous females to be present in the intertidal sample from June until February. As ovigerous females were never present during autumn (March - May) either the previous winter's adult females migrated into deeper waters or they died before the new season's females matured in the autumn. The peak of brooding occurred from June to August, i.e., during winter (Table 6.3).

(d) Egg development

N. ursus ova passed through four distinct stages of development, which are similar to those stages described for Manx majids (Hartnoll, 1963). Newly laid egg masses appear a bright orange-yellow which turns brownish-yellow and finally brown just prior to the eggs hatching. Individually, Stage 1 eggs were a yellow sphere composed of granular yolk while Stage 2 eggs contained a yolk area and a clear area of cleavage. Stage 3 eggs had rudimentary red eyes and pinkish chromatophores, and Stage 4 (pre-hatch) eggs had fully formed black eyes, silverish-black chromatophores and a reduced yolk sac. As I never managed to keep ovigerous females in the laboratory from egg-laying to hatching, I have no direct evidence on the development time of the eggs. However, Table 6.3 displays the data obtained from staging egg samples from all ovigerous females found during the field study. Stage 1 eggs first occurred in early

June while Stage 4 eggs first appeared in late July. Assuming that these are the same egg broods, development takes between 49 - 56 days. At this time of the year sea temperature in the intertidal area was approximately 8 - 10°C.

Table 6.3 The occurrence of the four egg stages in the *Notomithrax ursus* sample, Oaro Platform, December 1976 - December 1977.

Month	Egg Stage			
	1	2	3	4
June	11			
July 1	9	6		
July 2	3	7	1	2
August	2	2	2	1

(e) Larval development

Rearing decapod larvae is very problematical and was not carried out with *N. ursus*. However, Stage 4 eggs were found by late July; consequently, hatching probably occurs in August. In addition, very small (< 5 mm CL) and hence very young *N. ursus* are found in the intertidal area in October. Assuming that these Stage 4 eggs from July become the tiny crabs found in October, the larval development takes approximately 56 days and appears to occur in the plankton.

6.4 DISCUSSION

6.4.1 Life Cycle

The life cycle of intertidal *N. ursus* followed a seasonal pattern. Numbers were lowest during October and it was during this month that the size distribution data revealed that very small, presumably newly-settled crabs, were recruited into the channel. The modal CL group for the total population dropped to its lowest (15 - 19.99 mm CL) in November indicating that there was a large number of young recruited into the intertidal sample. In December the modal group rose to 20 - 24.99 mm CL and there was a slow

increase in the mean CL until February. Examination of the soft crabs during the November to December period showed that crabs were passing through successive prepuberty moults indicating that this was the juvenile growth period.

There was no sex difference in the mean CL of *N. ursus* except in February when the males were significantly longer than females. As there was no increase in moulting, especially to post-pubescence, at this time, this difference in February must have been caused by the influx of large males from outside the intertidal area (i.e., from deeper water). Thus, contrary to the situation in the majids *Libinia emarginata* (Gray, 1957) and *Leptomithrax longipes* (Roper, 1975) with *N. ursus* there is no difference in mean body length attributable to sexual dimorphism.

During March, juvenile crabs began their moult to puberty and there was a marked increase in the mean CL of females. Coupled with the influx of adult males, this moult to puberty resulted in an increased mean CL for the total sample and an increase in the modal group to 25 - 29.99 mm CL. The influx of crabs reached its maximum in April. Females continued to moult to puberty during May and the modal group of the total sample increased to 30 - 34.99 mm CL.

In June, females showed a significant increase in mean CL and the mean size of *N. ursus* reached a maximum of 31 mm CL suggesting that the moult to puberty for the sample was completed by that month. The lack of moulting during June to August may be the result of inhibition caused by the colder temperatures (see Carlisle, 1957, on *Carcinus maenas*) or because the puberty moult of *N. ursus* (which has seasonal life cycle) is also the terminal anecdysis. The latter is suggested by the following facts:

(1) Post-pubescent crabs were frequently found carrying epizoic animals such as tube worms, while epizoic animals were never found on prepubescent crabs.

(2) Post-pubescent exuviae were never found in the laboratory nor the field while prepubescent exuviae were found frequently.

(3) Post-pubescent crabs were never seen in the process of moulting (= proecdysis) while prepubescent crabs were.

(4) Post-pubescent crabs were never found with regenerating appendages, only with scar tissue; prepubescent crabs with limb buds were found quite frequently.

(5) During handling in the laboratory or the field, post-pubescent crabs rarely autotomised appendages while prepubescent crabs readily cast limbs.

(6) Terminal anecdysis is a typical majid feature (Berry & Harntoll, 1970; Hartnoll, 1963, 1965, 1968; Hinsch, 1972; Knudsen, 1964a).

The copulatory sequence observed in *N. ursus* is very similar to that described in *Pugettia producta* by Knudsen (1964b). In all cases the position was female-over-male which is typically used by the Majidae (Knudsen, 1964b).

Although copulation occurred between intermoult crabs in the laboratory in May, June, October, November, and January, the majority of copulation probably occurred in the field between March and May since females began to mature in March and adult males were already present. As females were capable of sperm storage, courtship could have commenced as early as February when the adult males entered the channel and the juvenile females were getting ready to moult to puberty. Mounding was unlikely to facilitate the mating of males with soft females as has been suggested for other majids (Carlisle, 1957; Ritchie, 1970) since there was no correlation between the occurrence of mounding and the moult of puberty, soft crabs never being found in mounds.

Egg-laying began in June. If copulation occurred when the females moulted to puberty then the ovaries of post-pubescent females take 6 - 8 weeks to mature. Alternatively, mating occurs immediately prior to egg-laying when the moult of puberty is complete. The former occurrence is suggested by Hartnoll's (1965) finding that in newly moulted post-puberty Manx and Jamaican majids the ova are still immature. Hinsch (1968) also found that ovarian maturation only occurs after the moult of puberty in *Libinia emarginata*. However, Watson (1972) reported that female *Chionoectes opilio*, newly moulted to maturity, generally laid eggs within 24 hr after mating.

The peak of brooding among *N. ursus* occurred from early July until the end of August (i.e., during winter) which is in direct contrast with

majid crabs of the Northern Temperate Zone who have a peak of brooding during summer (Lebour, 1927; Hart, 1960; Knudsen, 1964a; Hartnoll, 1965; Hinsch, 1972). As the peak of brooding occurs immediately after the peak of the puberty moult for the intertidal *N. ursus* sample, it is probably correlated with the initial insemination of the newly moulted adult females. The fact that adult females kept in the laboratory (for over four weeks) without males were capable of laying fertile eggs, combined with the fact that a female, which was observed to copulate in the laboratory, laid eggs within 24 hours of mating, suggests that *N. ursus* females are capable of sperm storage.

A few ovigerous females were found until March suggesting that *N. ursus* can raise more than one brood/year. The absence of eggs from March to May suggests that females which reproduced the previous winter die off during the autumn - or they do not ovulate again until the new season's females mature. Consequently, females survive for a minimum of 20 months. Males may survive for two or more years, as adult males joined the sample in February, before the new season's males matured.

The 56-day period of larval development suggested by the results of this study seems plausible when compared to the results of Webber & Wear (1981) who managed to rear *N. ursus*. Although none of the six reared *N. ursus* specimens moulted to the first crab stage, 40 days elapsed between hatching and the death of the last surviving megalopa.

6.4.2 Migration

The mean size and modal group of the sample remained at the June levels until August when they both dropped and, during September, the mean CL for males dropped significantly. This rapid drop in the mean carapace size of the sample suggests that adult *N. ursus* migrate out of the area (to deeper water?) or die. As adult males rejoined the sample the following February, their absence from the intertidal area was not due to their death but to their migration. The seasonal fluctuations in the sex ratio of the intertidal *N. ursus* sample were undoubtedly attributable to these migrations inshore in autumn and to deeper water in spring.

Inshore - offshore migration has also been observed in other majids (Stebbing, 1893; Yoshida, 1941; Katoh *et al.*, 1956; Vernet-Cornubert, 1958; Knudsen, 1964a; Pereyra, 1966, 1968; Stevcic, 1967; Ritchie, 1970; Musick &

McEachran, 1972; Winget *et al.*, 1974) and other crabs (Bainbridge, 1960) and may be attributed to several possible causes. The sudden influx of adults followed by the moult to puberty of juveniles and then egg-laying suggests that *N. ursus* migrates inshore to breed, as is the case with *Maja squinado* (Stevcic, 1967), *Chionoectes opilio* (Yoshida, 1941; Katoh *et al.*, 1956), *Jacquinotia edwardsii* (Ritchie, 1970). However, as ovigerous females are found in the intertidal region at other times of the year, and the males remain in the intertidal region for several months after brooding begins, the migration may be correlated with food abundance, as is the case with *Pugettia producta* (Knudsen, 1964a). It seems most likely that the inshore migration shown by *N. ursus* results from both breeding and feeding requirements as has been found to be the case in *Chionoectes tanneri* (Pereyra, 1966) and *Pisa tetraodon* (Vernet-Cornubert, 1958).

6.4.3 The Role of the Mask in Breeding

The only instance of 'courtship' which was observed gave ambivalent data on the role of the mask in precopulatory behaviour. The male failed to mate the female. Was it because he was unmasked or did his soft exoskeleton prevent him from overcoming her resistance? Perhaps the male was not strong enough to position the pair. Alternatively, the female may not have been receptive because she was brooding. This is not very likely in view of the fact that in two other majids, *Pugettia producta* (Knudsen, 1964a) and *Libinia emarginata* (Hinsch, 1968) ovigerous females have been observed to copulate prior to release of the larvae. The final possibility is that the unmasked metecdysed male was not attempting copulation at all but was perhaps attempting to steal algae from the female. This explanation seems unlikely in view of the fact that in other odd instances crabs have been seen to steal a piece of algae from another crab with relative ease.

The male continually grasped and released the algae and associated holding hairs of the female and this may be the 'palpation' which Hartnoll (1968) maintains occurs prior to copulation between males and hardened female majids. Was it the hairs or the algae which were important? I suspect that the hairs would be of major importance as these are thought to be sensory in both *N. ursus* (Maryan, pers. comm.) and *Hyas lyratus* (Wicksten, 1976) and more chemo-tactile information

would be conveyed by contacting the hairs, not the algae. Ryan (1966) demonstrated that the non-majid *Portunus sanguinolentus* (Herbst) had a sex-attractant in the urine of the female and initiation of courtship by pheromones was suggested in the majid *Libinia emarginata* (Hinsch, 1968). Consequently, it is possible that the male *N. ursus* who flapped their abdomens in response to the female may have responded to a pheromone of the female, released perhaps in her urine. If male *N. ursus* are attracted to a pheromone emitted by the female, this chemical is unlikely to be simulated by the application of an algal mask which has no fixed species composition.

The lack of any definitive courtship was quite probably the result of unfavourable conditions in the laboratory. Although Hartnoll (1968) maintained that some majids have no courtship, caution in reaching this conclusion might be prudent. In other animals, complex and distinctive display behaviour went undetected until extensive detailed studies were carried out specifically concerned with documenting display repertoires (Wilson, 1975; Jackson & Pollard, 1982).

Actual copulation seemed unaffected by the mask as in mixed groups of intermoult masked/unmasked individuals where crabs had a choice of partner, copulation occurred regardless of the mask. In addition, Chapter 5 showed that there was no change in the amount or composition of the mask during the peak copulation period. If copulation does occur between males and newly moulted females the mask would not be involved as the females would at most be only partially masked.

Brooding also seemed to have no reliance on the mask, in fact, there seemed an inverse correlation with brooding females being covered with less algae. As mentioned previously, this is probably due to the time spent cleaning and aerating the eggs, lessening the time available for masking activities.

6.4.4 The Role of the Mask Against Possible Predation

The smallest crabs recruited into the intertidal area were heavily masked. Although the larval stages were not obtained, the size and the fact that these crabs were recruited into the sample so soon after the eggs were hatched suggests that *N. ursus* masks immediately it reaches the

first crab stage. This hypothesis is supported by Lebour (1928) who found that the larvae of the Plymouth majids masked themselves with any foreign matter available directly they came out of the megalopal skin. Interestingly, Lebour also found that the non-masking non-majid crabs *Cancer, Atelecyclus, Thia, Xantho* and *Pilumnus* all masked initially, the former two up to the third and fourth young stages; after which they usually ceased. However, the swimming crabs did not mask at all. Lebour (1928, p.501) hypothesised that -

> "the very young are so helpless that it is a great advantage to hide instead of fleeing. The swimming crabs being able to swim beautifully almost directly they emerge from the megalopa, do not need to cover themselves in this way".

Lebour's hypothesis attains considerable credibility if one considers that the young of *Sepia* (Wells, 1958) and *Octopus cyanea* (Wells & Wells, 1970) hatch with a pre-set, very rigid 'crab-shaped' prey image. Initially the young cephalopods only attack crab-shapes, but the range of shapes attacked widens with age. Presuming for the moment that New Zealand octopuses do prey on *N. ursus*, and their young do have a set 'crab-shape' prey image, then it will be advantageous for young *N. ursus* to be heavily masked immediately they settle. The pressure to be masked would theoretically lessen as *N. ursus* got larger, since the octopuses which were capable of attacking them would have a wider food range. In addition, larger *N. ursus* would be better able to defend themselves.

Upon completion of moulting, soft crabs are immediately unmasked and hence susceptible to predation if the mask is a procrypsis. As intermoult *N. ursus* take a minimum of 24 h to re-mask, one would expect newly moulted crabs to take longer as their exoskeleton requires at least 48 h to harden. However, the data presented in Chapter 5 showed that extremely soft, and hence newly moulted crabs, were partially to fully masked. Wicksten (1975a) also observed that *Loxorhynchus crispatus* began masking within 24 h of moulting. A partial explanation for this surprising ability to mask while soft, may be found in the fact that *N. ursus* (Dell, 1963) and *L. crispatus* (Wicksten, 1975a) have both been observed to remove algae from their exuviae. Removing an already cut piece of algae from the exuvium would require less effort than seeking and cutting a fresh piece of alga. Even so, the selection pressure to mask must be intense to overcome the difficulties of masking while the exoskeleton is so soft.

Moulting was confined to September (i.e., spring) through to May (autumn), with the bulk of moulting occurring from November to April. An interesting correlation is that the European *Octopus vulgaris* (Boycott, 1954) moves inshore during spring until autumn. The Kaikoura fishermen also hold that octopuses are most prevalent in the shallow water catches during spring until autumn. The starfish *Coscinasterias calamaria* (Crump, 1969) and the sea lion *Neophoca forsteri* (Ritchie, 1970) are known to change their diet to *Macrophthalmus hirtipes* and the majid *Jacquinotia edwardsii* respectively when mass moulting occurs in these crabs. It is therefore feasible that the inshore movement of these octopuses is also correlated with the moulting of crabs. Consequently, the young intermoult *N. ursus* would need to be more heavily masked than the *N. ursus* found during June to August and this was found to be the case (Chapter 5).

The increased vulnerability of newly moulted *N. ursus* was not found to be associated with mounding behaviour as has been proposed for other majids (Carlisle, 1957). However, the results suggested an association between the formation of mounds and the general vulnerability of *N. ursus* to predation as was observed in *Maja squinado* (Baal, 1953; Stevcic, 1971). During experiments with predatory octopuses, using variable backgrounds (see Chapter 14), 'mounds' occurred eight times in the presence of an octopus when no cover was available, and only once when cover was available. In addition, in two of the three cases that *N. ursus* formed 'mounds' after being stressed by human interference these crabs lacked background cover.

The 'mounds' formed by *N. ursus* were much smaller than those reported for other majids (e.g., Ritchie, 1970). It may be that the 'mounding' behaviour observed is not the same as that reported for other majids but is the result of these crabs trying to hide themselves, in the absence of cover, by excavating (see Chapter 8) under other individuals. Alternatively, as *N. ursus* were never observed to leave the water voluntarily, the size of the 'mounds' may have been limited by the water level, which on all occasions where 'mounding' occurred was never deeper than approximately five crabs. For example, the five crab 'mound' shown in Plate 6.1 reaches from the rock on which it was formed to the water surface.

In conclusion, the data indicate that the mask is not involved with the intraspecific behaviours involved in breeding, but that it is related to size, with smaller crabs being more heavily and more consistently masked. As smaller, younger crabs are more vulnerable this suggests that the mask is involved in providing protection.

SECTION I

CHAPTER 7

POTENTIAL FACTORS FAVOURING MASKING

7.1 INTRODUCTION

Masking behaviour by *Notomithrax ursus* was not correlated with breeding (Chapter 6). However, differences in the body area masked were related to the size of the crab (Chapter 5), indicating that the mask may be a protective adaptation to either the physical environment (e.g., against desiccation or water turbulence) or to other animals, which may be potential competitors, predators or prey. The initial step in determining which selection pressures are responsible for masking behaviour was to determine if *N. ursus* was indeed ever exposed to them, bearing in mind that 'exposure' involves the dimensions of both time and space.

When investigating the duration of exposure one must consider that organisms dwell in a rhythmic environment in which there are a number of natural frequencies: 24 h daily cycles, 24.8 h lunar day cycles, lunar related fortnightly and synodic monthly periods, and seasonal or yearly changes (Brown, 1960). These rhythms are reflected in an animal's activities, both physiological and behavioural, and intertidal animals, like *N. ursus*, are most affected by seasonal, lunar and diurnal oscillations of environmental conditions (Allen, 1966). In addition, there are inter-related factors affecting rhythms (see Allen, 1972 for examples).

The most revealing rhythm to study to determine the exposure of *N. ursus* to selection pressures was locomotory activity as *N. ursus* must move in order to feed, mask and interact with other animals. For example, it is generally known (Cott, 1940; Edmunds, 1972) that the value of even the best camouflage is greatly reduced by movements that make the camouflaged animal conspicuous.

As the rhythms of predators and prey are generally synchronised (Curio, 1976), a knowledge of the diurnal locomotory rhythm of *N. ursus* was especially important in determining if the mask is a protective device

against predators or prey. For example, if the mask acts as visual eucrypsis then *N. ursus* would be best protected if they spent the day (when visibility is comparatively good) resting motionlessly in an appropriate environment and were active only at night (when visibility is comparatively poor) (Edmunds, 1974).

Although many studies have investigated diurnal locomotory activity, there have been relatively few involving intertidal animals (e.g., Park *et al.*, 1941; Fingerman & Lago, 1957; Guyselman, 1957; Fielder, 1965; Bregazzi & Naylor, 1972a, b; Coombs, 1972; Kanicruk & Herrnkind, 1973; Al-Adhub & Naylor, 1975) and even fewer involving crabs (e.g., Naylor, 1958, 1960, 1961; Atkinson & Naylor, 1973; Honnegger, 1973a, b). This paucity of studies is possibly a reflection of the many difficulties involved in detecting and measuring locomotory activity of aquatic animals over long periods.

While daily locomotory rhythms are an important part of the biology of any species, one must also consider the time - space relationship, dispersal: what is the duration of exposure in any particular location? Seasonal migrations have previously been discussed in Chapter 6. However, *N. ursus* may also undergo short-term dispersal (duration > 1 day but < 1 year). In addition, a knowledge of the daily movements of individuals is a necessary prelude to the study of social systems [interactions in animals (Hazlett & Rittschof, 1975)]. For example, if the individuals of a species do not restrict their movements to a particular portion of their environment they could not be territorial and social hierarchies can only develop if the composition of the group(s) is stable.

Of the methods available for obtaining information about short-term animal movements (within a defined area), providing individuals with identifiable marks is one of the most commonly used. Capture - recapture methods assume that the animals do not lose their marks and that the sample animals are classified correctly as marked or unmarked. However, the crucial assumption on which all capture - recapture estimates depend is that all live individuals are equally at risk to capture (Cormack, 1968).

The spatial component of the exposure of *N. ursus* to selective forces concerns two different aspects: their distribution on the shore and their dispersion.

Many animals are found in crevices, holes, or buried in the substrate. Such hidden animals are called 'anachoretic' (Edmunds, 1974). Anachoretes can be hidden for all or only part of the time and do not require other defences whilst hidden. If *N. ursus* remains hidden all of the time, it would be unlikely to need to be cryptic as well, so it would be necessary to look for another function for the algal mask. Since anachoresis can be achieved by burying in the substrate or hiding under rocks or amongst the algae, the utilisation of these three forms of cover by *N. ursus* was investigated.

A knowledge of anachoretic behaviour was important for a further reason. Tidal fluctuations, as found in the intertidal area, cause water turbulence which can conceivably unbalance or invert *N. ursus*. As the algal mask covers only the dorsal surface, then its function, whether signalling or cryptic (anti-signal), will be dependent on *N. ursus* remaining dorsal side up. If *N. ursus* are not anachoretic and hence are exposed to water turbulence, then it is conceivable that they will require a stabilising mechanism and the mask may fulfil this function.

If the mask is crypsis, especially eucrypsis (visual, tactile, chemical, or even auditory, Edmunds, 1974), then *N. ursus* would need to be closely associated with the algae. Alternatively, if the mask has noxious or toxic properties then *N. ursus* need not be closely associated but they must still be close enough to the algae in order to mask with it and so that predators/prey are familiar with its properties. Finally, if the mask is a signal, then to achieve the contrast necessary for contrast, *N. ursus* needs to be disassociated from the algae resembling that present in the mask. Hence, it was necessary to determine the relationship of *N. ursus* to the algal cover present in the environment.

The size of 'individual distances' (Crook, 1963) determines how animals are spaced in the environment (i.e., dispersion). On the basis of experimental evidence, Tinbergen *et al.* (1967) concluded that the impact of predators may be, at least, partly responsible for the phenomenon whereby well camouflaged species live at interindividual distances which greatly exceed the distance from which predators usually detect them directly. This advantage to disperse would apply whether the predators were using an area-restricted searching technique or if they were hunting by searching image (Tinbergen, 1960). On the same principle, anachoretic animals

should not be too abundant or predators using an area-restricted searching technique may learn to find them (Edmunds, 1974). In addition, McBride (1971) suggested that individual distance must always be included as a factor in the study of social behaviour, in which the mask may conceivably play a role. Consequently, a knowledge of the dispersion of *N. ursus* was necessary to elucidate the possible selection pressures responsible for maintaining masking behaviour.

Spider crabs, in general, are solitary (Berry & Hartnoll, 1970). However, dispersion is not always constant, but will vary in accordance with biological rhythms (Leyhausen, 1971). Seasonal rhythms in particular are generally correlated with other parameters, especially those associated with breeding. Thus it was important to study not only how *N. ursus* are dispersed but also when they are dispersed/grouped. If *N. ursus* do form groups, it would also be advantageous to know the sex/size/maturity composition of the groups. This information will help to determine if dispersion is associated with social parameters. However, dispersion can also be density-dependent (Bovbjerg, 1959). Consequently, any changes in the dispersion of *N. ursus* may also be related to the density of the population.

7.2 METHODS

7.2.1 Field Study

Initially, information regarding locomotory activity, anachoresis, and dispersion was collected during the general field study, outlined in Chapter 3. Locomotory activity was gauged by recording which of the *N. ursus* found were moving out in the open when encountered and the activities they were engaged in. Anachoresis was determined by recording how *N. ursus* were associated with the available substrate and algal cover and whether or not they were buried, and the effect of the tides was determined by recording whether or not *N. ursus* were submerged (Table 7.1). Dispersion was determined by recording the individual numbers of any *N. ursus* aggregated in the same algal clump or crevice, under the same rock or, if exposed, within 4 cm (= approximately one crab length) of one another. From this it was possible to check the records and find the sex, size, maturity, and species of neighbouring *Notomithrax*.

Table 7.1 Distribution characteristics measured to determine the utilisation of the habitat by *Notomithrax ursus* in the study channel, Oaro Platform.

Category	Characteristics	
Rock cover	Under a rock	Crab covered by lump of mineral > 20 cm^2
	On a rock	Crab perched on a rock devoid of algae
	No rock	
Algal cover	In algae	Crab under, or positioned among, an algal clump
	Algae present	Algae not touching crab but present within a 5 cm radius
	No algae	No algae within 25 cm radius of the crab
Substrate	In substrate	Only the dorsal carapace showing above the substratum
	On sand	Crab resting on mineral particles < 1 mm^2
	On gravel	Crab resting on mineral particles > 1 mm^2 and < 1 cm^2
	On stones	Crab resting on mineral particles > 1 cm^2 and < 20 cm^2
	On bedrock	Crab resting on continuous sheet of limestone
Submergence	Submerged	Crab completely immersed in water
	Not submerged	Crab partially or not immersed in water

Dispersal required a special field study and was conducted in the same channel as used for the general field study at Oaro Platform. The channel was divided into five areas, on the basis of pre-existing physical characteristics (Fig. 7.1), and monitored for five days in February 1978. Each day *N. ursus* were hand captured, differentially marked, and their sex, maturity, ovigerous state, and size were recorded. The crabs were then replaced where caught. Marking was achieved by a combination of dyeing the crab with Nile blue and/or painting the ventrum with nail polish. Both methods of marking had previously been tested in the laboratory and were found to be both long-lasting and non-harmful to *N. ursus*. The marking combinations used (Table 7.2) allowed intrachannel movements to be monitored as well as emigration/immigration. Noting any peculiarities of the crabs, such as misshapen or scarred chelae, also aided individual recognition of marked crabs.

In addition to monitoring the channel, the neighbouring channels and pools were spot-searched each day to check on the possible transverse movement of marked crabs. As the marking techniques had lasted over five weeks in the laboratory, the channel was again monitored a fortnight after the termination of marking crabs.

As the general field study was only conducted during daylight hours, additional observations were conducted at night at the Oaro Platform and the Wooloomooloo channel. Observations were made on nine separate occasions between July 1977 and March 1978 with the aid of a spotlight covered with red cellophane and recorded using a portable tape recorder. When a *N. ursus*, which was away from mineral or plant cover, was located, its activity was recorded until it again sought cover. The distance between exposed crabs and any interactions between them were also noted. This information was used as part of the dispersion study. The observers made no effort to systematically search among the algal and mineral cover for *N. ursus*, but random checks were carried out.

Nocturnal observations of locomotory activity presented several difficulties. The whole period of low tide needed to fall in complete darkness, observations were restricted to a maximum of 4 h (usually 3 h) per tide, and red light made observation difficult. In addition, there was a possible disturbance of the animals by the observer. In view of these difficulties and the fact that *N. ursus* were only being observed during low tides, locomotory activity was also studied in the laboratory

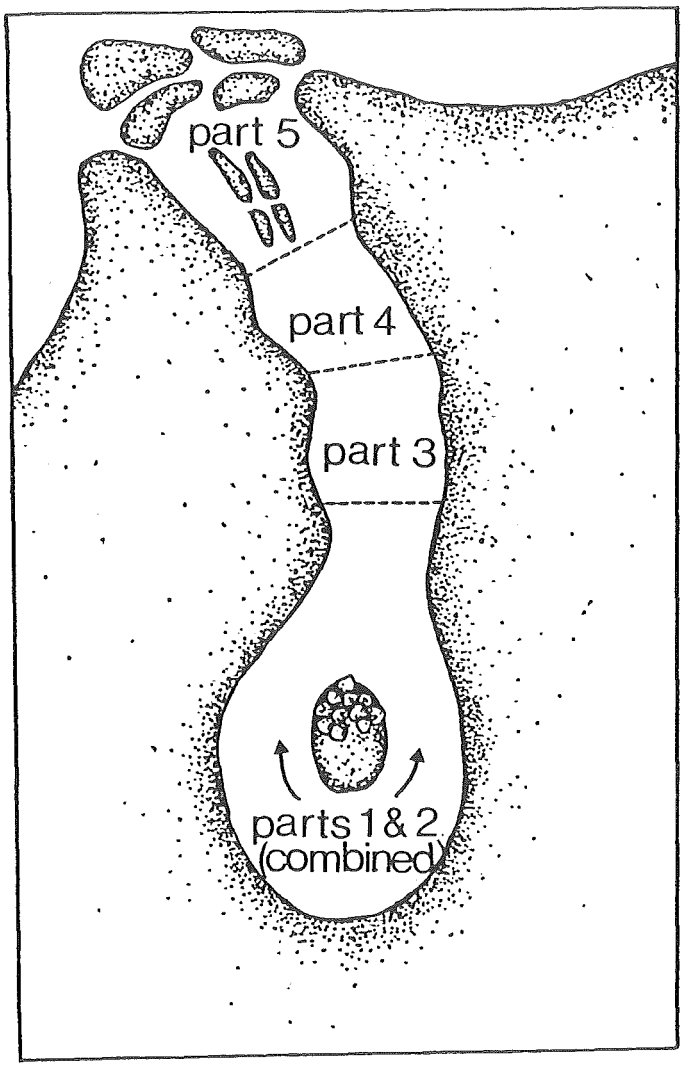


Fig. 7.1 Division of study channel, Oaro Platform for the study of crab dispersal (5 - 23 February 1978).

Table 7.2 Modes of differentially marking *Notomithrax ursus* found at Oaro Platform, 5 - 9 February 1978.

Channel Part	5/2/78	6/2/78	7/2/78	8/2/78	9/2/78
Parts 1 & 2	Nile blue	Nile blue	-	-	Nile blue
	red spot on left posterior ventrum	-	black stripe on telson	red stripe on telson	-
Part 3	Nile blue	Nile blue	-	-	Nile blue
	red spot on right posterior ventrum	-	black spot under left chela	red stripe on telson	-
Part 4	Nile blue	Nile blue	-	-	Nile blue
	red spot under right chela	-	black stripe ventrally across 4th pair pereiopods	red stripe on telson	-
Part 5	Nile blue	Nile blue	-	-	Nile blue
	red spot under left chela	-	black spot under right chela	red stripe on telson	-

by means of a special experiment. Information regarding anachoresis, dispersion, and water cover was also gleaned from observations made during the locomotory activity period (see below), agonistic encounters (Chapter 8), and the interactions between *N. ursus* and octopuses (Chapter 14).

7.2.2 Locomotory Activity Experiment

Locomotory activity was investigated using an actograph (Sollberger, 1965) which consisted of a Rigouchi revolving recording drum which could revolve once/24 h or once/7 days. Against the drum was a cartridge pen recorder, balanced on a fulcrum, and attached to a physiology wheat straw. The fulcrum was equipped with an adjustable lead counterweight to cope with individual variation of the crabs. One end of a length of cotton thread was tied around the carapace of a *N. ursus* between the second and third pereiopods. The other end of the thread was secured to the tip of the physiology straw. The crab was then placed in the centre of a circular bowl (26 cm diameter) containing fresh aerated sea water, a layer of gravel for traction, and a hiding place made with two stones arranged so that the crab could only enter and leave the same way. This method, which satisfied the criteria outlined by Coombs (1972), allowed the crab to move unimpeded and any possible friction was alleviated by the counterbalance (see Fig. 7.2). Although gravel was found infrequently in the study area, *N. ursus* showed no aversion to resting on or in gravel where it occurred in the field or laboratory (see later). Gravel was used in preference to mud or stones as the former made the water turbid when the crab moved, impeding observations, and the thread caught among the stones when there were too many of them.

Movements of the crab caused deflection of the marking pen. Observations of the working system revealed that the size of each deflection was directly proportional to the force of the causative movement. The minute variations of the recorded line during periods of inactivity were the result of respiratory and slight body movements as opposed to locomotory activity.

N. ursus had access to *ad lib.* feeding prior to experimentation and each individual was recorded for 24 h.

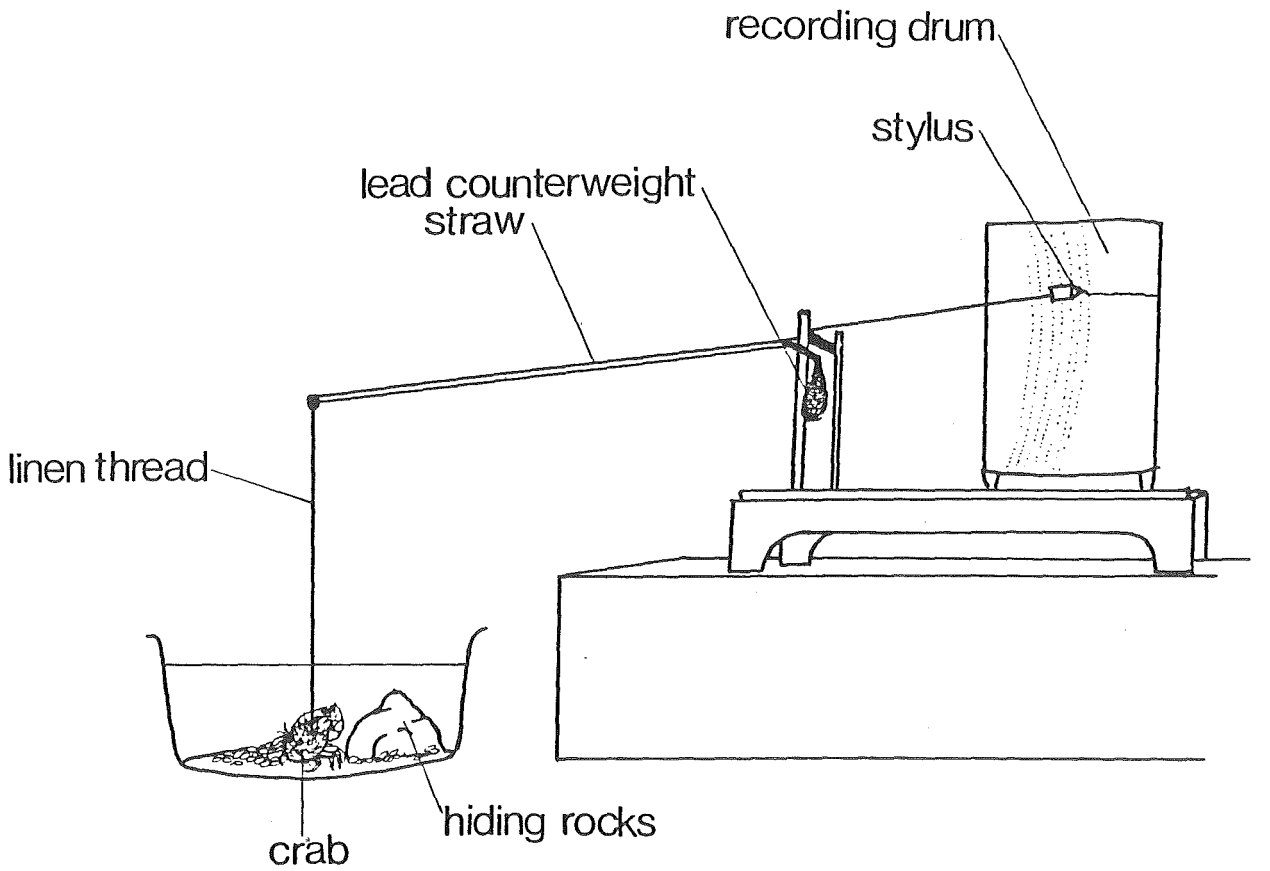


Fig. 7.2 Actograph used for recording activity of *Notomithrax ursus*.

(a) Controlled light regime (LD)

The actograph was enclosed in a lightproof casing and kept at a room temperature of 18°C ± 2°C. Lighting was provided by an Osram 40W bulb (emitting 175 lux at 6 cm depth measured by a Gossen light meter) and set on a 10 : 14 h light : dark regime. The light regime approximated the mean prevailing natural light conditions during this period.

Seventeen trials were conducted between July - September 1977 using six female *N. ursus* (CL 29.25 - 33.75 mm) and six males (CL 29.05 - 47.25 mm). Five of the 12 crabs were given two consecutive trials to control for acclimatisation effects. Individual crabs were kept in the laboratory for 4 - 24 days prior to experimentation.

(b) Natural light regime (nLD)

Since the results were to be interpreted ecologically it was important to keep conditions as natural as possible. In the initial 17 trials the difference between light and dark was abrupt, and the light had a constant intensity level and a different spectral composition than natural light. These conditions gave no indication of whether *N. ursus* showed a gradual change in locomotory activity in response to a gradual change in illumination, or whether they were only active during total light or darkness. In addition, the expression of any tidal rhythm may have been masked by the length of time some of the crabs were held in the laboratory prior to use.

Consequently, the experiment was re-run at the Edward Percival Field Station. The actograph was no longer enclosed but was situated by a large window. The effects of movement disturbance were minimised by separating the experimental area from the remaining area of the room by polystyrene sheeting. Since the experimental aquarium was supplied with running sea water piped directly from the ocean there were probably daily temperature and salinity fluctuations comparable to, but not as marked as, those in the natural environment. As the water level in the aquarium was constant, the influence of changing water pressure and depth during the natural tides was eliminated. Crabs were used within seven days (usually one day) of being collected.

Table 7.3 Comparison of *Notomithrax ursus* out from cover during night low tides compared with those present during the previous daylight low tide.

Date	Area	Observation time (hours)	Crabs out	Crabs present during previous daylight low tide	*N. ursus* population exposed (%)
31/ 7/77	Wooloomooloo	2.0	3	?	-
27/ 8/77	Oaro	1.5	2	21	9.5
19/10/77	Wooloomooloo	1.0	None	?	-
13/11/77	Wooloomooloo	2.0	None	?	-
14/11/77	Oaro	1.0	2	15	13.3
5/ 2/78	Oaro	1.75	9	71	12.7
6/ 2/78	Oaro	1.25	4	45	8.9
7/ 2/78	Oaro	1.0	7	51	13.7
22/ 3/78	Oaro	1.5	4	48	8.3
TOTAL		13.0	31	231	12.1

Twenty-one trials were conducted between November 1977 and July 1978 using six female *N. ursus* (CL 23.0 - 35.0 mm) and five males (CL 28.45 - 34.95 mm). Ten of the eleven crabs were given two consecutive trials to control for acclimatisation effects.

Following Fielder & French (1970), activity estimations were made by partitioning each 24 h record into hourly periods and then measuring the duration of activity bursts for each hour. The data for all subjects were pooled for each hourly period and the mean activity/hour was calculated and then plotted against the hour of the day. Since the activity records were initiated at different times of the 24 h period, the data for the LD experiment were rearranged so they all started at the same time. In the nLD experiment, the data for 4 h either side of the first and last light were used to determine the amount of crepuscular activity. Tidal activity was determined from the nLD data for 2 h either side of high and low tide.

7.3 RESULTS

7.3.1 Locomotory Activity

(a) Field observations

Of the 940 crabs located during daylight low tides, only 0.4% (4) were not under cover. Of these four non-anachoretic crabs, one was stationary whilst the other three were walking. It is quite possible that *N. ursus* normally move under cover, but these three were caught crossing open areas.

During the night low tides no crabs were observed away from cover on two occasions, and only 31 crabs were found exposed on the other seven occasions. Conditions at night were too difficult to accurately determine the number of *N. ursus* present in the channel, but random investigation showed that many more *N. ursus* were present under cover. Consequently, the number of crabs found at night was compared to those found during the nearest daylight low tide immediately following or preceding the night tide in question (Table 7.3). Less than 14% of the

N. ursus population present (at least during the nearest daylight low tide) were exposed during night tides.

(b) Laboratory experiments

(i) Controlled illumination (LD). Changes in locomotory activity, as shown by a typical *N. ursus* under controlled illumination and measured by the actograph are shown in Plate 7.1. Comparison of these periods of activity shown by individual *N. ursus* with the external tides at the time of experimentation revealed no superimposed tidal rhythm (see Plate 7.1). However, *N. ursus* were more active at night than during the day (Fig. 7.3). The mean latent period for activity to commence after the cessation of illumination was 82 min, whilst the mean latent period for activity to cease after the onset of illumination was 38 min (Fig. 7.3). Hence the Zeitgeber (cue) for the locomotory activity rhythm appears to be the change in illumination. If the latent periods are discounted, there is a considerable difference between activity displayed during darkness (mean *minimum* activity shown for any hour of darkness was 58%) and that displayed during illumination (mean *maximum* activity shown for any hour of illumination was 10%).

(ii) Natural illumination (nLD). *N. ursus* were again active during darkness and inactive during illumination throughout all 21 trials. As the ratio of hours of darkness to hours of illumination varied, results were analysed and represented in terms of 4 h prior to and following the first and last illumination. Fig. 7.4 shows the mean crepuscular activity/hour for *N. ursus* in these terms. Mean activity was greater than 70% in the 4 h of darkness before and after illumination. During the 4 h period of illumination following first light and that preceding last light, mean activity was never greater than 20%. Mean activity dropped 20% during the first hour prior to first light and then 55% to first light, then slowly decreased as light increased. The reverse occurred around last light.

A qualitative examination of the activity recordings and the corresponding solar radiation charts obtained during the nLD experiment revealed that the amount of activity an individual expressed was inversely proportional to the amount of incident light.

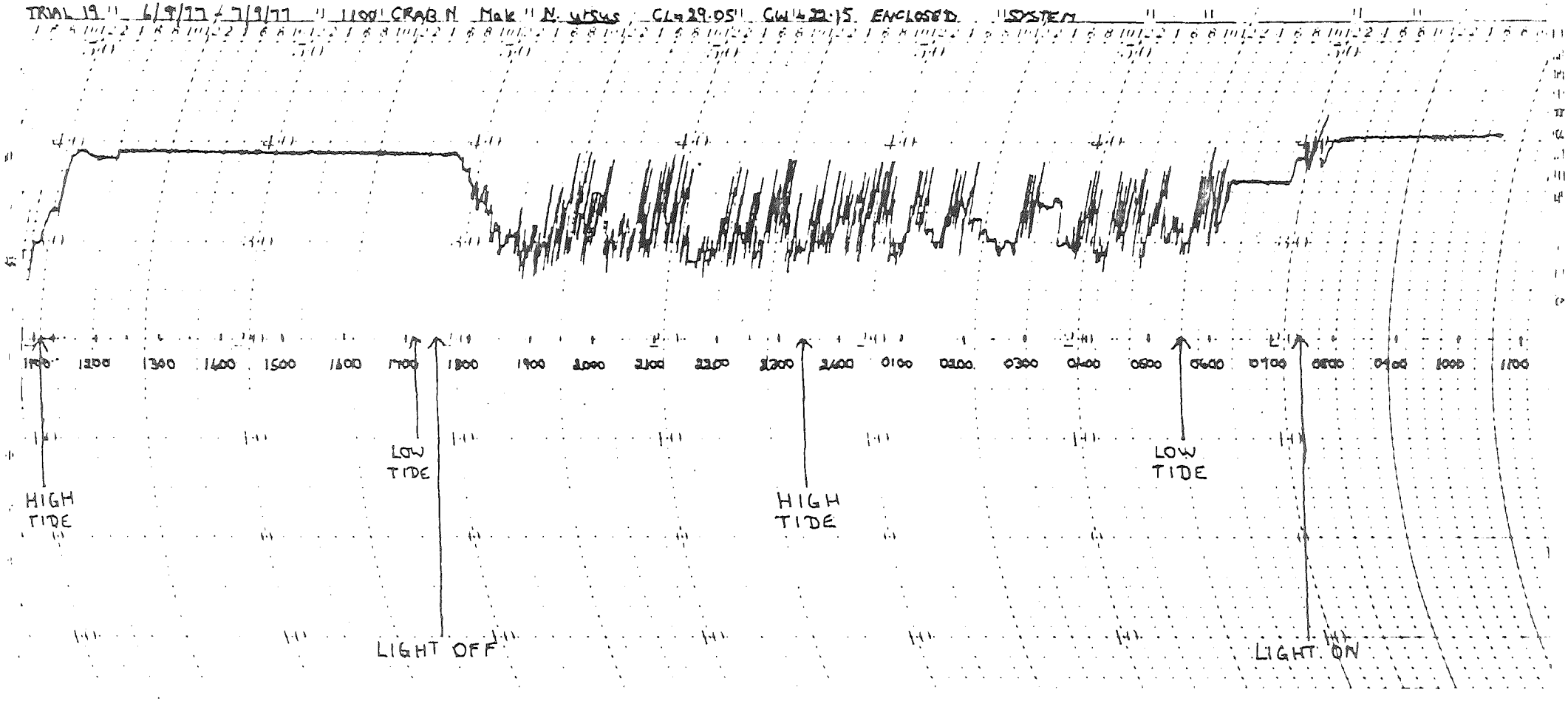


Plate 7.1 Actograph recording showing the influence of illumination on the activity of *Notomithrax ursus*.

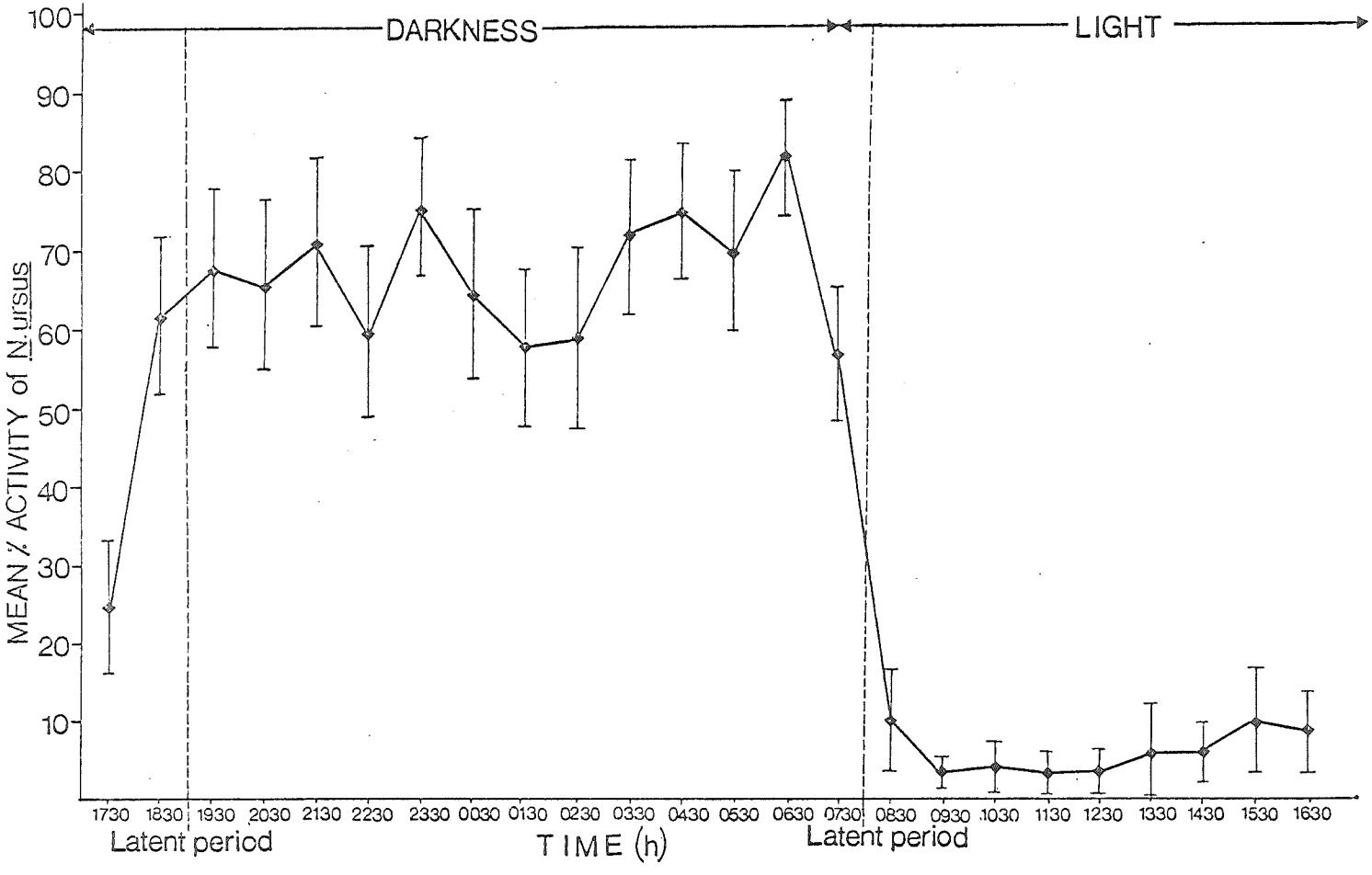


Fig. 7.3 The effect of illumination on the mean activity of *Notomithrax ursus* over 24 h. Bars are twice standard error.

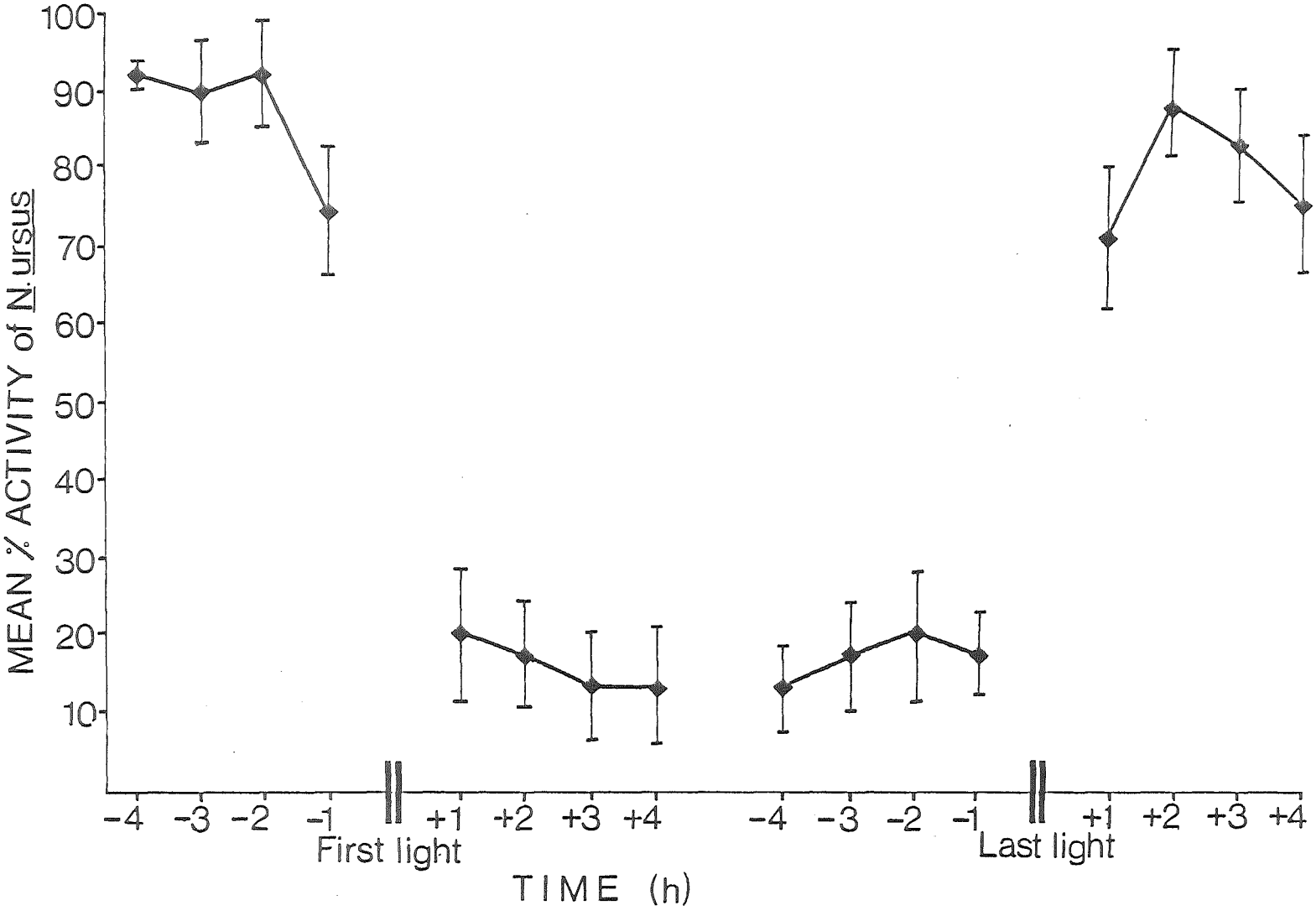


Fig. 7.4 Crepuscular activity of *Notomithrax ursus*. Bars are twice standard error.

There was no superimposed tidal rhythm on the spontaneous locomotory activity. Fig. 7.5 shows that mean activity was greater than 70% during darkness and less than 35% during illumination regardless of the tidal cycle.

Casual observations of *N. ursus* in the laboratory holding tanks also showed *N. ursus* to be inactive during periods of illumination. When suddenly exposed to light, these crabs would immediately seek cover. Under red or very dim white light *N. ursus* would emerge from cover and become active. Masked crabs appeared to move around more than unmasked *N. ursus*, especially when there was a lot of background cover.

7.3.2 Dispersal

The abundance of *N. ursus* in the channel changed not only from month to month (see Chapter 6) but also from day to day (see last column Table 7.4). These daily fluctuations in abundance were most likely the result of natural immigration/emigration. However, they may have been partly the result of the marking agents which, although they had no physiological effect on *N. ursus* in the laboratory, may have increased *N. ursus*'s chances of predation in the wild. For example, they may have made *N. ursus* more conspicuous, even though only the ventral surface was marked, or the marking agents may have made *N. ursus* more active and hence more exposed. The daily fluctuations in abundance were unlikely to be a result of the searching technique as it was unlikely that more than one or two crabs were missed. In addition, the seasonal data (Chapter 6) suggest that the daily fluctuations were unlikely to be caused by the natural death or recruitment of the young.

Assuming that all the crabs present in the channel on any particular day were captured and marked, then the number of crabs migrating to or from the channel can be calculated. If the number of crabs marked on the first day is T, and the number of marked crabs re-captured the following day is R, then the number of crabs which emigrated by the second day is $T_1 - R_1$. Accordingly, the number of crabs which have immigrated into the area by the second day is $T_2 - R_1$. The migration of *N. ursus* to and from the channel was frequent (see Table 7.5). Thirty-three to sixty-two percent of the sample immigrated into the channel, while a slightly higher percentage emigrated (47 - 76%), resulting in an overall loss of crabs over the period monitored. A comparison of the percentage of emigration with the previous

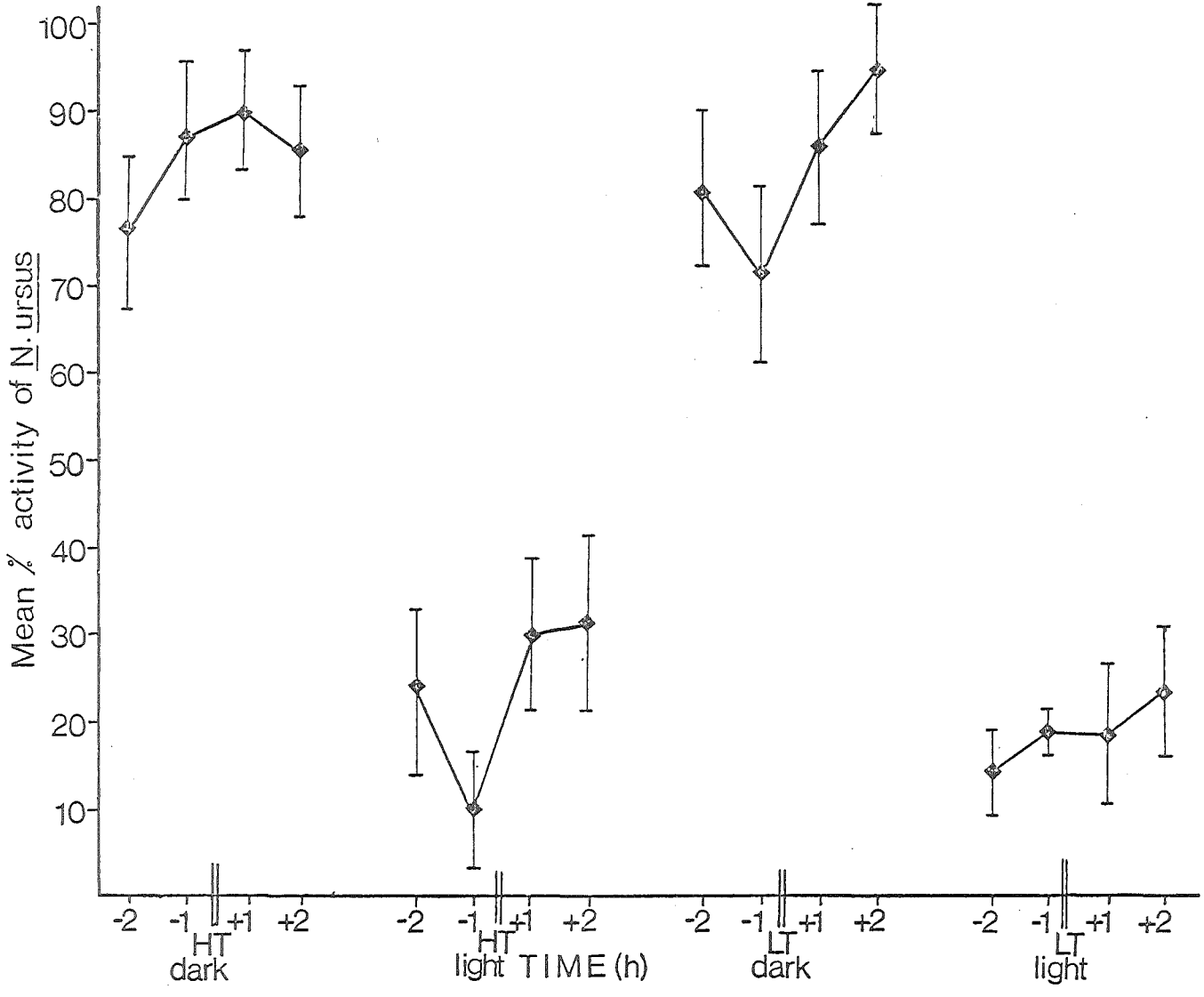


Fig. 7.5 Mean activity of *Notomithrax ursus* compared with external tidal changes over 24 h.

Table 7.4 Abundance of *Notomithrax ursus* found in the study channel at Oaro Platform, 5 - 23 February 1978.

Date	Channel				
	Part 1 & 2	Part 3	Part 4	Part 5	Total
5/2/78	18	18	15	20	71
6/2/78	4	8	22	11	45
7/2/78	8	13	17	13	51
8/2/78	6	11	9	6	32
9/2/78	10	5	5	6	26
23/2/78	19	13	6	10	48

Table 7.5 Migration of *Notomithrax ursus* to and from the study channel at Oaro Platform, 5 - 9 February 1978.

N. ursus	5/2/78	6/2/78	7/2/78	8/2/78	9/2/78
Stationary (marked)	-	23.94% (17)	53.33% (24)	39.2% (20)	38.89% (14)
Emigrated by (lost)	-	76.06% (54)	46.67% (21)	60.78% (31)	61.11% (22)
Immigrated by (new)	-	62.2% (28)	52.9% (27)	33.0% (12)	46.2% (12)
Days total	71	45	51	36	26

day's density (Table 7.6) suggested that density may have affected dispersal in three out of four cases. A comparison of the percentage of crabs emigrating daily with the mode of marking those crabs (Table 7.7) shows that the increased emigration may also have been attributable to the marking techniques. Nail polish would appear to have a more detrimental effect than the Nile blue dye, and a combination of the two markers had the worst effect.

Some (24 - 53%) *N. ursus* remained in the channel. As time passed, the number of the original sample remaining in the channel gradually

declined from 19.6% to 9.86% (Table 7.8). The lower numbers remaining from the later days (7 and 8 February) may have been the result of multiple handling of the crabs.

Table 7.6 Comparison of density of *Notomithrax ursus* with their subsequent emigration from the channel at Oaro Platform, 5 - 9 February 1978.

	5/2/78	6/2/78	7/2/78	8/2/78
Density	71	45	51	36
Percentage emigration	76	47	61	61

Table 7.7 Comparison of mode of marking *Notomithrax ursus* with their subsequent emigration from the channel at Oaro Platform, 5 - 9 February 1978.

	5/2/78	6/2/78	7/2/78 & 8/2/78	
Mode of marking	Painted & dyed	Dyed	Painted	
Percentage emigration	76	47	61	61

Although 9.86% of the original crabs were still in the channel after 96 h there was a possibility that these crabs did not remain in the channel for the whole of the five days but that they migrated in and out of the area. Recording the sex, maturity, size, and any peculiar characteristics for each *N. ursus* enabled individual identification of the crabs which then allowed a determination of whether the same crabs were present from day to day (Table 7.9). Of the eligible population, 15% remained in the channel for 48 h, while 4.79% remained for 72 h, and only 1.41% remained for 96 h.

The discrepancy between the number of marked crabs found on subsequent days and the lengths of consecutive time each individual crab stayed in the channel, indicated that crabs returned to the channel. Examination of the

movement records for individual crabs shows this assumption to be correct: 13.79% of *N. ursus* left and then returned to the channel and 7.04% returned twice.

Table 7.8 Marked *Notomithrax ursus* recaptured in the channel at Oaro Platform, 5 - 23 February 1978.

Marked on	Recaptured after				
	24 h	48 h	72 h	96 h	18 days
5/2/78 (71)	23.9% (17)	14.08% (10)	12.68% (9)	9.86% (7)	1.41% (1)
6/2/78 (45)	31.1% (14)	15.6% (7)	2.2% (1)	-	-
7/2/78 (51)	7.8% (4)	3.9% (2)	-	-	-
8/2/78 (32)	12.5% (4)	-	-	-	-
Total	19.6% ($^{39}/_{199}$)	11.38% ($^{19}/_{167}$)	8.62% ($^{10}/_{116}$)	9.86% ($^{7}/_{71}$)	

Table 7.9 Marked *Notomithrax ursus* consecutively recaptured in the channel at Oaro Platform, 5 - 9 February 1978.

Marked on	Consecutive hours present			
	24	48	72	96
5/2/78 (71)	26.8% (19)	1.41% (1)	0	1.41% (1)
6/2/78 (45)	15.56% (7)	11.1% (5)	0	-
7/2/78 (51)	1.96% (1)	3.92% (2)	-	-
8/2/78 (32)	12.5% (4)	-	-	-
Total	15.58% ($^{31}/_{199}$)	4.79% ($^{8}/_{167}$)	0% ($^{0}/_{116}$)	1.41% ($^{1}/_{71}$)

No marked crabs were found in areas surrounding the channel during daylight random checks. However, one male *N. ursus* (CL 38 mm) was found during the night tide of 7 February 1978. This crab had markings from 7 February 1978 so it had moved at least 40 m in 12 h.

The ratio of *N. ursus* present in the different channel parts varied from day to day (Table 7.4). In view of the negative results from the random checks across the platform, the ratio changes were unlikely to be attributable to transverse movements by *N. ursus*. Consequently, longitudinal movement within the channel was investigated. This was made feasible by the differential marking of each day's sample according to the channel part. After 24 h, 14% of the eligible marked crabs were recaptured in the same channel part, while 7% were recaptured in the same part after 96 h (Table 7.10). Twelve percent of the eligible population remained in the same channel part for 48 h and 3.6% remained for 72 h (Table 7.11).

Analysis of individual crab movement sequences revealed that only 1.8% of the marked sample returned to the SAME place in the channel during the 96 h it was monitored, and that they only returned once, not twice.

Table 7.10 Marked *Notomithrax ursus* recaptured in the same channel part, Oaro Platform, 5 - 23 February 1978.

Marked on	Recaptured after				
	24 h	48 h	72 h	96 h	18 days
5/2/78 (71)	18.3% (13)	11.27% (8)	9.86% (7)	7.04% (5)	1.41% (1)
6/2/78 (45)	20.0% (9)	6.67% (3)	0 (0)	-	-
7/2/78 (51)	5.88% (3)	3.92% (2)	-	-	-
8/2/78 (32)	9.38% (3)	-	-	-	-
Total	14.07% ($^{28}/_{199}$)	7.78% ($^{13}/_{167}$)	6.03% ($^{7}/_{116}$)	7.04% ($^{5}/_{71}$)	

Table 7.11 Marked *Notomithrax ursus* consecutively recaptured in the same channel part, Oaro Platform, 5 - 9 February 1978.

Marked on	Consecutive hours present			
	24	48	72	96
5/2/78 (71)	19.72% (14)	2.82% (2)	0	0
6/2/78 (45)	15.56% (7)	4.44% (2)	0	-
7/2/78 (51)	1.96% (1)	3.92% (2)	-	-
8/2/78 (32)	6.25% (2)	-	-	-
Total	12.06% ($^{24}/_{199}$)	3.59% ($^{6}/_{167}$)	0	0

7.3.3 Anachoresis

(a) Field work

(i) Daylight low tides. During daylight low tides, 940 *N. ursus* were found in the study channel at Oaro between December 1976 and December 1977. Of those crabs, 99.47% were under rocks ($\chi^2_{[1]} = 920$, $p < 0.005$) while 99.5% were associated with but not under algae ($\chi^2_{[2]} = 1856$, $p < 0.005$) and 98.61% were on, rather than buried in, the substrate ($\chi^2_{[1]} = 888.7$, $p < 0.005$). As only 0.5% of the sample were not under rocks, it was impossible to determine if the lack of rock cover changed the crabs' algal or substrate affiliation. The small percentage of crabs found exposed indicates that these individuals were probably caught in transit between hiding places rather than preferring to be away from cover.

Only 0.4% of the crabs found were not anachoretic, that is, not under rocks, algae nor buried in the substrate; hence, only 0.4% of the sample was potentially exposed to other animals. One crab (0.1%) was partially exposed as it was not under a rock nor in the substrate, but it was under an algal clump (see Fig. 7.6).

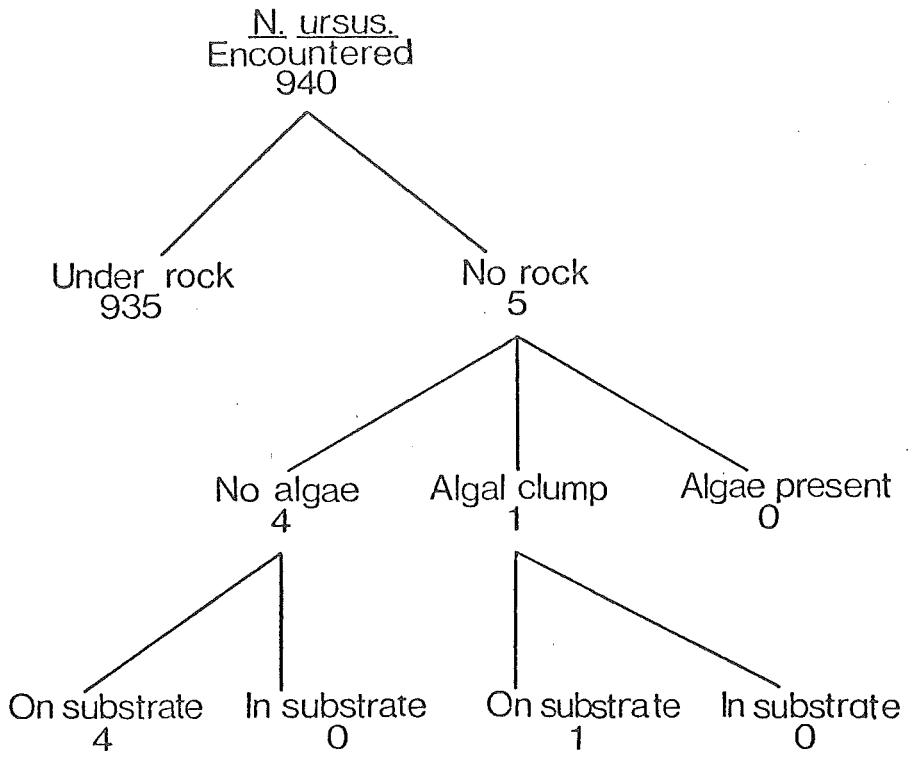


Fig. 7.6 Substrate utilisation by *Notomithrax ursus* in study channel, Oaro Platform (1976 - 1977).

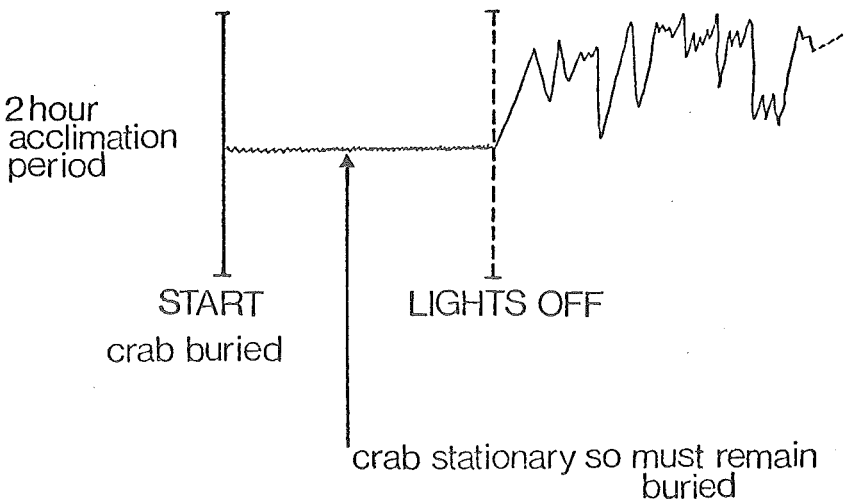


Fig. 7.7 Tracing of actograph recording showing continued inactivity of buried *Notomithrax ursus* during illumination.

Of the 927 crabs found resting on the substrate, there was no significant difference ($\chi^2_{[2]} = 0.304$, $p > 0.5$) between those resting on sand (32.36%), stones (30.74%), or bedrock (31.71%). Although there was a significant difference between those found on gravel (5.18%) and those on other substrates, the difference was probably attributable to the fact that there was very little gravel present in the study channel. The supposition that the difference was caused by lack of gravel rather than lack of preference by *N. ursus* is corroborated by the fact crabs utilise gravel in areas (e.g., Spaniards Bay) (see Fig. 3.2) where it is plentiful. This absence of preference by *N. ursus* means that, provided the crabs are given access to cover, any of the above substrates can be used in the laboratory tanks.

(ii) Night low tides. Anachoresis was not systematically studied at night, but a random investigation showed crabs to be present, mainly under rocks but a few were in algal clumps. Two of the crabs found exposed at night were attempting to excavate (see below for definition).

(b) Laboratory work

(i) Daylight. During daylight *N. ursus* in the laboratory usually remained hidden. If removed from under cover, they immediately sought cover again under rocks, algae or other suitable objects. If unable to get underneath an object *N. ursus* "hid" next to it, keeping some portion of its body in contact with the object. When no object was available, *N. ursus* remained next to the side of the container and did not venture out into the middle unless provoked. This type of anachoretic behaviour has also been observed in the shrimps *Alpheus heterochelis* and *A. normanni* (Nolan & Salmon, 1970). In the total absence of available cover, *N. ursus* were often observed to 'excavate' (see below) certain substrates creating a hollow in the substrate into which they disappeared as far as possible.

Excavating Behaviour

By flexion of the cheliped C-M* joint, the chelae were adducted until they almost met under the anterior of the body. The body and the chelipeds were then lowered by flexing the AL's* at the C-M joint. The chelae were then pushed down into the substrate and propelled forward by an extension of the C-M joint and sideways by an extension of the basis-ischium (B-I) joint. In fine-particle substrate, removal of material

* C-M = carpus-merus, AL = ambulatory leg (also see Fig. 8.1)

was effected by the rapid extension of the C-M joint once the merus was perpendicular to the carpus, causing the particles to be "shovelled" away by the broad propodus (= manus). In these finer substrates, excavation was often aided by AL1 and AL2 which had the same action as the chelipeds except that AL1 was extended laterally about 45° and AL2 laterally approximately 90°. The "shovelling" action was aided by the extension of the remaining ambulatory legs at their C-M joints.

In coarse-particle substrates, a chela grasped an individual particle which was released at the point of fullest extension of the cheliped C-M joint. The rapid upward motion of the chela effectively flicked the particle away. When particles were actually grasped and not "shovelled" the chelae were often used alternately rather than in unison, and quite often, only one chela was employed for the task.

The body was braced by, and pivoted on, the AL4's and often the AL3's as well. Additional support was often gained by positioning the posterior of the body and the AL4's against a vertical surface such as a rock. As the depression was enlarged, the AL's on one side and then the other gradually moved down into it causing the crab to rock from side to side. Excavation continued until the crab was buried, with only the eye-stalks and raised central dorsum being left above the surface.

(ii) Darkness. Observations in the laboratory triple tank (Chapter 8) suggested a correlation between excavating behaviour and illumination. All 11 crabs (including three ovigerous, one non-ovigerous and one juvenile female, and an adolescent and two juvenile males) observed, excavated when the white light was on but not when the dim red or yellow 'safe-light' was used, indicating that *N. ursus* had a negative phototaxis. These observations were corroborated by the activity experiment: *N. ursus* were found buried in the gravel at the beginning of the trial (providing the crab had had an acclimation period) when the trial started in daylight, and at the end when the trial finished in daylight. Further, the lack of movement shown on the actograph recordings during periods of illumination indicated that, having excavated, *N. ursus* remained buried while subjected to illumination (Fig. 7.7). Excavating behaviour was observed to occur in the dark on two occasions during filming with a light intensifier (Chapter 8). On both occasions *N. ursus* had been stimulated between the fourth pair of legs by a glass rod suggesting that excavating may be a defence.

7.3.4 Dispersion

(a) Field work

(i) Daylight low tides. During daylight low tides, 32% of the *N. ursus* sample were found singly, while 68% had X number of neighbours within 4 cm (Fig. 7.8). Large groups were less common, with 45% of the population in groups of two to four, but only 23% of the population in groups greater than four. To determine whether the distribution was clumped or scattered, the coefficient of dispersion (CD) was computed using the following formula:

$$CD = \frac{\text{variance}}{\text{mean}} = \frac{S^2}{\bar{Y}} \quad \text{(Sokal \& Rohlf, 1969).}$$

In the present context:

$\bar{Y}$ = mean number of neighbours

$$= \frac{\text{total number of neighbours}}{\text{number of groups}}$$

To avoid confusion with the mean of non-grouped data, this value "$\bar{Y}$" will be termed "m", thus:

m = mean number of neighbours

and $CD = \frac{S^2}{m}$

The value of the CD will be near 1 in distributions that are essentially random, > 1 in clumped samples and < 1 in case of repulsion. As the CD for the total yearly *N. ursus* population was 4.56, *N. ursus* exhibited a clumped distribution ($\chi^2_{[4]}$, $p < 0.005$)*.

Computation of the CD's for the individual months revealed that the distribution of *N. ursus* varied seasonally. Individuals were scattered from September to December and clumped from January to August. This seasonal change in distribution was probably attributable to behaviours concerned with the life cycle and not to density (Table 7.12). There was a direct relationship between CD and the maximum group size, the influx of adult crabs, and the periods of suspected mating. However, there was no

---

* For the purposes of a chi-square test for goodness of fit (of observed to expected frequencies) no expected frequency should be less than 5 (Sokal & Rohlf p.88). Consequently, during the application of a Poisson distribution, the lower frequencies at one tail of the curve must be grouped. In the present case, groups 4 - 15 have to be combined and df = 5 — 1 = 4.

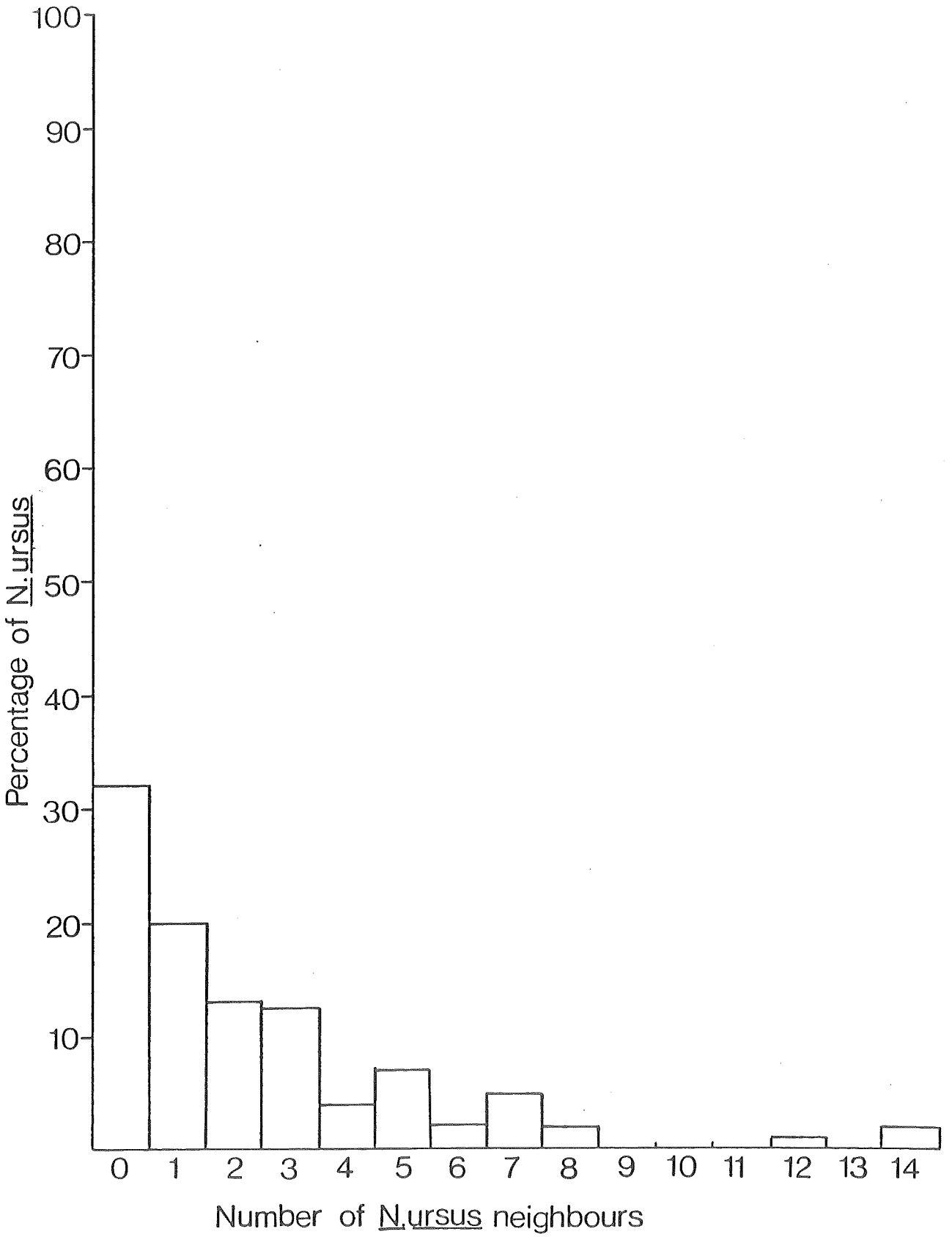


Fig. 7.8 Frequency of *Notomithrax ursus* which were aggregated within one crab length of 0 - 14 other *N. ursus*.

Table 7.12 Comparison between the monthly density, dispersion (CD), maximum group size, and life-cycle related behaviour of *Notomithrax ursus* at Oaro Platform, January 1977 - December 1977.

Month	Density	CD	Maximum group size	Life-cycle related behaviour
October	6	-	1	Recruitment of young
November	15	-	2	Prepuberty moults
December	23	-	2	Prepuberty moults
January	51	2.4234	6	Prepuberty moults
February	91	2.1849	6	Influx of large males
March	134	2.6529	8	Influx of large males - moult to puberty
April	168	6.5126	15	Influx of large males - mating (?)
May	130	3.1180	9	Moult to puberty - mating (?)
June	101	5.9660	13	Egg-laying/brooding - mating (?)
July 1	57	1.3121	6	Egg-laying/brooding
July 2	35	3.3016	6	Egg-laying/brooding - mating (?)
August	21	2.6920	6	Egg-laying/brooding
September	14	-	3	Adults migrate
TOTAL	846	4.5618		

relationship between CD and density. There was also a direct relationship between maximum group size and life cycle related behaviours, but not between maximum group size and density.

An examination of the composition of the groups found in the study channel (Table 7.13) shows that single sex groups were smaller, and less frequent than mixed groups, and all-female groups were restricted to the season when the puberty moult and mating occurred.

A comparison of the CD's for single sex and mixed groups (Table 7.14) shows some interesting correlations with the behaviours associated with life cycle (reported in Chapter 6). Clumping was negligible during the period October to December, when the newly settled young were recruited into the intertidal area (i.e., *N. ursus* has a scattered distribution when young). Males and females began to congregate in mixed groups in January. This may have been a result of increased density as both the population and individual crabs were growing. Coincident with their immigration in February and the puberty moult in March, males began to aggregate both with females and each other, but there were no corresponding all-female groups. In April, when males continued to immigrate into the channel and mating was presumed to occur, the population had a high incidence of both male and female single sex groups and an especially high incidence of mixed groups. During May, when the females and remaining immature males moulted to puberty, and during June when mating continues and egg-laying began, only mixed groups of *N. ursus* were evident. At the beginning of July, the males regrouped, while the females were scattered and mixed groups had a random distribution. By the end of July there was a high incidence of mixed grouping but no single sex grouping. In August the population had reverted to a random to scattered distribution and was completely scattered by September.

Significantly more mixed groups had a 1 : 1 ratio than had an uneven ratio for the whole year ($\chi^2_{[2]} = 52.809$, $p < 0.005$). There was an equal probability that the remaining groups had more of either sex than the other. An examination of the seasonal changes in the sex ratio of the groups (Table 7.15) indicated that, prior to suspected mating, the mixed groups had a 1 : 1 ratio or had more males than females. However, during the suspected mating periods, the mixed groups had a 1 : 1 ratio or had more females than males.

Table 7.13 Seasonal frequency of single sex and mixed groups of *Notomithrax ursus* in the study channel, Oaro Platform, January 1977 - December 1977.

Month	Size of mixed male-female groups 2	3	4	5	6	7	8	9	13	15	Total	CD
October												-
November	1										1	-
December	1										1	-
January		1	4		1						6	1.5260
February	5	5	1	2	1						14	2.9962
March	8	7			1	1	1				18	2.7826
April	17	2	3	2	1		2	1		1	29	9.1692
May	5	4	2	1	2	1	2	1			18	4.4977
June	5	6	5	1					1		18	6.6260
July 1	3	3	4		1						11	1.0222
July 2	3		2		1						6	3.8095
August			1	1	1						3	1.0
September												-
TOTAL	48	28	22	7	9	2	5	2	1	1	125	

Month	Size of all-female groups 2	3	4	Total	CD	Size of all-male groups 2	3	4	Total	CD
October					-					-
November					-	2			2	-
December					-	2			2	-
January	1			1	-	1			1	-
February	3			3	-	2	1		3	1.9997
March	8			8	-	1	1	1	3	1.4204
April	3	1	1	5	2.5999	1	1		2	3.8340
May	5	1	1	7	0.9281	4	1		5	0.8
June					-	2			2	-
July 1					-	1	1		2	2.9940
July 2					-	1			1	-
August					-	1			1	-
September					-		1		1	-
TOTAL	20	2	2	24		18	6	1	25	

Table 7.14 Comparison between the monthly density, CD of mixed and single sex groups, and life-cycle related behaviours of *Notomithrax ursus* at Oaro Platform, January 1977 - December 1977.

Month	Total density	CD Females	CD Males	CD Males/Females	Life-cycle related behaviour
October	6	-	-	-	Recruitment of young
November	15	-	-	-	Prepuberty moults
December	23	-	-	-	Prepuberty moults
January	51	-	-	1.5260	Prepuberty moults
February	91	-	1.9997	2.9962	Influx of large males
March	134	-	1.4204	2.7826	Influx of large males - puberty moult
April	168	2.5999	3.8340	9.1692	Influx of large males - mating (?)
May	130	0.9281	0.8	4.4977	Puberty moult - mating (?)
June	101	-	-	6.6260	Egg-laying/brooding - mating (?)
July 1	57	-	2.9940	1.0222	Egg-laying/brooding
July 2	35	-	-	3.8095	Egg-laying/brooding - mating (?)
August	21	-	-	1.0	Egg-laying/brooding
September	14	-	-	-	Adults migrate

Table 7.15 Seasonal changes in the sex ratio of *Notomithrax ursus* groups in the study channel, Oaro Platform, January 1977 - December 1977.

	Group	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July 1	July 2	Aug.	Sep.	TOTAL
Equal ratio	1M : 1F		1	2		5	8	17	5	5	3	3			49
	2M : 2F				2	1			1	1	2	2	1		10
	3M : 3F							1			1				2
	4M : 4F							1							1
	Total	0	1	2	2	6	8	19	6	6	6	5	1	0	62
More females	1M : 2F					1	1	2	2	2	2				10
	: 3F				1			2	1	2	2				8
	: 4F					1		1	1						3
	: 5F												1		1
	: 7F						1								1
	2M : 3F									1					1
	: 4F								2			1			3
	: 6F								1						1
	3M : 4F								1						1
	: 5F							1	1						2
	4M : 5F							1	1						2
	: 9F									1					1
	5M : 10F							1							1
	Total	0	0	0	1	2	2	8	10	6	4	1	1	0	35
More males	2M : 1F				1	4	6		2	4	1				18
	3M : 1F				1			1		2					4
	: 2F					1		1					1		3
	4M : 2F					1	1								2
	: 3F						1								1
	5M : 1F				1										1
	Total	0	0	0	3	6	8	2	2	6	1	0	1	0	29

In March, prior to the suspected first mating, post-pubescent males grouped with the prepubescent females (Table 7.16), while during April and June the mixed groups contained increasingly more mature non-ovigerous and Stage 1 ovigerous females. During July, males grouped with ovigerous females bearing Stage 1 and Stage 2 eggs and later Stage 3 eggs.

Table 7.16 The percentage of different female classes of *Notomithrax ursus* found grouped with males at Oaro Platform, January 1977 - December 1977.

Month	Percentage of female classes grouped with males						Total
	Juvenile	Adult - eggs carried externally					
		None	Stage 1	Stage 2	Stage 3	Stage 4	
March	96.4	3.6					28
April	70	30					60
May	30.8	69.2					52
June	2.8	71.4	25.7				35
July 1	5	30	35	30			20
July 2	20	10		60	10		10
August	11.1	11.1	22.2	22.2	11.1	22.2	9
November	100						1
December	100						2

(ii) Observations during night low tide. Of the 31 *N. ursus* observed out from cover at night, 67.74% had no other *N. ursus* within a radius of at least 100 cm. The other 32.26% had other *N. ursus* within 100 cm of them and 22.58% were within 15 cm of conspecifics. Four (57%) of these neighbouring crabs were interacting (three were displaying; one was retreating). The remaining 43% (3) 'neighbouring' crabs were sitting motionless within 15 cm of one another. Three of 31 exposed crabs were within 15 cm of the related masking crab *N. peroni* but there was no observed interaction between the two species; two of the *N. ursus* sat motionless and the other fed among *Corallina* algae.

(b) Laboratory work

Behaviour in the laboratory triple tanks was consistent with that in the field: *N. ursus* dispersed (as far as the tank area would allow) under red light 'darkness' and grouped and/or hid during daylight (Table 7.17).

Table 7.17 The dispersion of *Notomithrax ursus* observed during the study of intraspecific agonistic behaviour (Chapter 8).

N. ursus	Light off	Light on	Light off	Light on
8 large males		- stood close - displayed if facing - excavated		
6 males 2 large 2 medium 2 small	- went to opposite corners of tank sections and moved about	- stopped moving except large one who displayed to own image in glass then sat close to medium one	- all began moving again	- all stopped moving - three sat together
6 females 2 juveniles (F1) 2 medium sized 1 medium ovigerous (F3-6) 1 large (F2) 1 large ovigerous (F3-6)	- went to opposite corners of tank sections and moved about	- 2 large, 1 medium and 1 small all began excavating - 2 medium and small sat posterior-to-posterior - other medium and small continued to move		
7 mixed 1 large male 1 ovigerous female (F3) 1 medium male 1 mature female (F2) 2 small males 1 immature female (F)	- initially clumped the moved about	- stopped moving within 7 min except medium male who attempted to copulate with ovigerous female		

7.3.5 Water Cover

(a) Field work

(i) Daylight low tides. Significantly more of the 940 *N. ursus* found during daylight low tides in the study channel were under water (97%) than were not (3%) ($\chi^2_{[1]} = 8.2634$, $p < 0.005$). Of the 28 *N. ursus* which were not under water, 100% of them were in shallow pools under the rocks. Consequently, none of the 940 *N. ursus* found was exposed to desiccation.

(ii) Night low tides. All 34 crabs found out of shelter were still completely submerged.

(b) Laboratory work

In the laboratory crabs were generally kept in water deeper than found at low tide in the study area. Although *N. ursus* often clung to the sides of the tanks just under the air/water interface, they were never observed to leave the water.

7.4 DISCUSSION

N. ursus was nocturnally active; the increased locomotory activity during darkness was reflected by both observational data and laboratory recordings. In the field, 0.4% of the sample were exposed during daylight low tides while only 0.3% were actually moving. Even during the night low tides activity was still low, only 14% of the presumed available *N. ursus* were exposed. In the laboratory, the artificial light conditions in the LD experiment differed to a considerable extent from those in the nLD experiment: for instance, dawn and dusk were absent, and the light had a different spectral composition and a constant intensity level. However, in spite of these differences, the crabs in artificial light showed the same characteristic activity pattern under light/dark conditions of similar length as those in nLD.

An abrupt change in light intensity, especially under controlled illumination, resulted in a correspondingly abrupt change in mean activity. Conversely, a gradual change in illumination resulted in a gradual change in activity. Hence, the probable Zeitgeber (cue) for the spontaneous locomotory activity rhythm exhibited by *N. ursus* was a change in illumination. Hagerman (1970) found the same to be true of *Crangon crangon*, and Bregazzi & Naylor (1972a, b) found that the locomotory rhythm of *Talitrus saltator* was synchronised by light/dark fluctuations and the animal was active during the dark period. *N. ursus* can be considered photonegative as under a controlled light regime the onset of illumination resulted in a change in activity twice as fast as the cessation of illumination (mean latent period: 38 : 82 min). In addition, *N. ursus*, both in the field and in the laboratory, immediately sought cover if exposed to white light.

Another strong influence on many biological rhythms, especially among intertidal marine animals, is that of the lunar day or tidal cycles. *Palaemon elegans* and *P. serratus* (Rodriguez & Naylor, 1972), *Crangon crangon* (Al-Adhub & Naylor, 1975), *Carcinus maenus* (Naylor, 1958), and *Uca crenulata* (Honegger, 1973a, b) all have a circatidal (i.e., combined circadian/lunar cycle) control. However, *N. ursus* exhibited no superimposed tidal rhythm regardless of the interval between an individual's capture and its being tested, or of the 'artificiality' of the experimental procedure. Naylor (1961) found that the effect of the tidal cycle on the marine crabs *Carcinus maenas* and *C. mediterraneus* was linked with the amount of tidal fluctuation to which the crabs were exposed. *N. ursus* ranges from the intertidal region down to 40 fathoms, the depth at which it occurs being dependent upon a combination of both the season and the crab's age (Chapter 6). However, *N. ursus* is always found submerged and hence the intertidal population can reasonably be expected to respond to illumination changes rather than those changes associated with the lunar cycle.

Many other environmental factors can influence an organism's rhythms. The activity rhythms of *Crangon vulgaris* (Hagerman, 1970) and the lobster *Panulirus argus* (Kanicruk & Herrnkind, 1973) are affected by season. However, there was no detectable difference in the activity (recorded by the actograph) shown by *N. ursus* in February (summer) or in June/July (winter).

Temperature may also affect the phasing of rhythms (Bregazzi & Naylor, 1972a, b). During the LD experiment temperature was held constant and thus could have no effect. However, during the nLD experiment the temperature was approximately that of the ocean and was subject to minor variations/trial. Trials conducted during winter when water temperature was colder, showed no differences in mean activity than those conducted during summer.

The effects of barometric (atmospheric) pressure on spontaneous locomotory activity were not investigated in this study. However, Guyselman (1957) found that barometric pressure fluctuations exerted no influence on the 24 and 12.4 h (i.e., exogenous) activity cycles of the crayfish *Cambarus virilis*. Although, Frank & Meyer (1972) found that activity level of *Hemigrapsus oregonensis* and *H. nudus* increased with decreases in environmental salinity, the effects of salinity were not investigated in this study.

The *N. ursus* sample present in the Oaro study channel was subject to daily fluctuations in abundance, caused by a natural immigration and emigration of individuals. Although emigration may be influenced by the marking technique, dispersal appeared to be related directly to the initial density, the amount of emigration being greater in larger groups. This density dependence of emigration suggests that it is important that *N. ursus* are dispersed which, in turn, suggests that they engage in agonistic behaviour (Bovbjerg, 1959; McBride, 1971). If one assumes that movement involves increased exposure to predation, then *N. ursus* are vulnerable. However, their exposure would be greatly reduced if the majority of movement occurs under the cover of rocks and/or algae, a possibility that is suggested by the fact that in the field only 14% of the available population were out from cover during their nocturnal activity period. In addition, movement does mean that an individual was exposed for only a limited time to the 'dangers' of any particular area.

The recapture rate declined with time. Of the crabs marked, 23.9% were recaptured after one day, 9.8% after five days, and only 1.41% after 18 days. These recapture rates were low compared to the 90% obtained by Hazlett *et al.*, (1974) for the crayfish *Orconectes virilis*. However, these animals were comparatively non-mobile and were contained in a

relatively 'bounded' area. George (1965) in a survey of mark-recapture studies involving mobile species and/or large populations in an 'unbounded' portion of an aquatic environment, found 23% to be the highest recapture rate.

The identification of individual crabs showed that 15.5% of the population remained in the study channel for two consecutive days, while 4.8% remained for three. Fourteen percent of the crabs who initially left returned to the channel, while 7% left and returned twice. Consequently, this 76% who initially left did not constitute a fixed group. This continual changing of the individuals present in the channel is not conducive to the animals forming a highly structured hierarchy of dominance so one would not expect *N. ursus* to have a particularly complex social system.

Although there was a lot of both intrachannel and extrachannel movement, 14% of marked crabs were found in the same channel part after one day, while 6 - 7% were found in the same channel part after 2 - 5 days. Twelve percent of the population were found in the same channel part for two consecutive days and 3.6% for three consecutive days. However, only 1.8% of the population returned to the same place in the channel. This extremely low incidence of *N. ursus* returning to the same place in the channel suggests that these animals do not have set resting places or refuges so it is unlikely that they will have territories (= defended areas).

The number of *N. ursus* marked in this study (225) was large compared to that in other studies (e.g., Hazlett (1975a) marked only 22 *Leptodius floridanus* and 21 *Hexapanopus angustifrons*). The immense variation in movement positions shown by *N. ursus* reinforces the point that a large sample is necessary to avoid gaining a false impression of a species' behaviour. If only a few *N. ursus* had been followed, or a lot had been followed for only a couple of days, the data may have suggested, for example, that *N. ursus* did not return to an area but continually moved.

N. ursus were completely anachoretic during daylight. If disturbed during periods of illumination, either in the field or the laboratory, they immediately sought cover. If cover was unavailable, they buried themselves by excavating the substrate. Excavating behaviour was

dependent on illumination and it did not occur during darkness unless the crab was exposed to 'predator-like stimuli' (see Chapter 8). This relationship between illumination and excavating behaviour reinforces previous findings that *N. ursus* are photonegative and suggests that these crabs are more vulnerable to mortality (probably from predation) during periods of illumination. *N. ursus* showed a marked preference for hiding under rocks rather than in algal clumps or the substrate. Assuming that predators are responsible then this preference is understandable as a predator would find it harder to extract *N. ursus* from under a rock, especially a large one, than from the algae or substrate.

N. ursus ventured from hiding at night in both the field and the laboratory, although they remained anachoretic for the majority of the time. Nolan & Salmon (1970) found that captive *Alpheus heterochelis* and *A. normanni* also spent the majority of their time completely hidden under shelter, but the tendency to remain concealed decreased at night when foraging took place.

If the mask does function as an anti-predator device, the fact that *N. ursus* were closely associated with algae suggests that the algal mask enables the crab to be cryptic as opposed to having toxic properties, or of being an advertisement. The question immediately arises, why does *N. ursus* need a cryptic camouflage if it is not exposed during times of good visibility? Firstly, the mask need not be crypsis against a visual predator. Alternatively, the visual predator may be a nocturnal one who possesses the ability to discriminate in dim light. Secondly, anachoresis may not be as effective against certain diurnal predators who have the ability to remove the shelter and flush the crabs out, but lack acute visual discrimination [e.g., the labrid fishes (Hobson, 1968)].

At night, whether in the field or laboratory, *N. ursus* maintained large individual distances when they were not anachoretic. For example, 67.74% of the crabs observed to be active at night were further than 33 crab lengths ($\simeq$ 100 cm) away from the nearest conspecific. Generally, the crabs avoided one another and, in the field, 57% of the crabs which were within four to five crab lengths of each other were engaging in agonistic display. These results suggest that dispersion of non-anachoretic crabs was important. If this distance maintained between *N. ursus* is greater than the predator's ability to detect, it would support the hypothesis that the mask is cryptic.

During daylight, *N. ursus* had an overall clumped distribution for the year, occurring in groups as large as 15. These crabs were also found in mixed groups, as large as 28, with the congeneric masking crab *N. peroni*. Congeneric groups are dealt with in Chapter 9. In the laboratory, and also in the May field sample, *N. ursus* huddled together in the absence of cover, often trying to get underneath each other. The behaviour of seeking contact was also, on occasion, observed to occur in the presence of hiding places.

This alternation between clumping and scattering has been recorded in other crabs. When out of water *Pachygrapsus crassipes* displayed little aggressive behaviour and aggregated, but in tide-pools there was no aggregating and aggression commenced at any close meeting (Bovbjerg, 1960a). Hazlett (1975b) found that in the hermit crab *Clibanarious tricolor*, individual distance decreased from almost 50 cm for individuals in low density populations to 5 cm in heterogeneous substrates (e.g., tide-pools and/or high population densities). Hazlett felt that the selective advantage was clear: where the population density is high an animal would spend all its time in agonistic interactions, and he felt the individual distance concept should be elaborated to one of multiple overlapping probability distributions. With *N. ursus* the change in individual distance was dependent on activity cycle rather than density: the crabs clumped when anachoretic and dispersed when active. This dependence on activity suggests that individual distance was involved with the maintenance of crypsis and not with the partitioning of resources such as shelter or food.

A consideration of the monthly dispersion figures showed that *N. ursus* were not always clumped during the day. Clumping was also dependent on the seasonal behaviour of *N. ursus*. During the non-breeding period of September to December, the intertidal *N. ursus* had a scattered dispersion, but during the breeding season of January to August they had a clumped dispersion. Although there were also marked differences in abundance between these two periods, the type of groupings formed during these periods confirmed that the dispersion was correlated with life cycle and not density.

The composition of the groups strongly suggested that the intertidal *N. ursus* sample had two mating sessions, one in April and one in late July.

Prior to April, males congregated with each other and with prepubescent females, while in early July males congregated with ovigerous females with Stage 2 and Stage 3 eggs. It is possible that the all-male groups, formed prior to suspected mating, were a form of 'lek' (Alexander, 1977) involving some form of competition for access to the females who are becoming eligible for mating. In addition, the combined groups may be the result of the males waiting to mate with the females immediately they become receptive. These hypotheses that there are two mating periods and that males may 'guard' the prereceptive females are corroborated by the sex ratio data. Prior to the suspected mating periods, the mixed groups had a 1 : 1 ratio or more males to females. During the suspected mating sessions, the sex ratio of the mixed groups was 1 : 1 or more females to males. Although there were not enough data for statistical analyses, these trends suggest that male *N. ursus* mate with more than one female.

As the majority of females in late July were ovigerous, this mating session appeared to be a second mating for the females mated in April as opposed to being the first mating for later maturing crabs. Also, as the females had Stage 2 and Stage 3 eggs, the data suggest that females can, and indeed do, mate when the brood is partly mature (see also Chapter 6). The occasional brooding female found in the intertidal area over summer suggests that the later migrating crabs may mate after migrating to deeper water or that they store sperm from their first mating.

N. ursus were not naturally exposed to desiccation by night or day and in the laboratory they were never observed to leave the water voluntarily. Consequently, it is highly unlikely that the algal mask is an adaptation concerned with protection from desiccation.

By virtue of their anachoretic behaviour, *N. ursus* were unlikely to be exposed to the effects of water turbulence. Also, as their strong, hooked dactyls enabled them to maintain a tenacious grip (Chapter 8) they were unlikely to be unbalanced if they did encounter any turbulence. In addition, when inverted, *N. ursus* adducted their legs, whose colouration and adventitious mask concealed the variegated ventrum. Consequently, it is highly unlikely that the algal mask is an adaptation for maintaining stability during water turbulence.

SECTION I

CHAPTER 8

ETHOGRAM OF *NOTOMITHRAX URSUS*

8.1 INTRODUCTION

To determine the function(s) of the mask of *N. ursus* it was necessary to obtain an ethogram, i.e., a detailed description of the typical action patterns along with descriptions of the situations in which these behaviour patterns occur. An ethogram enables an investigator to assess the most meaningful lines of evidence to pursue to the second stage of ethological analysis, i.e., the experimental investigation of the stimuli involved in the behavioural interactions (Hazlett, 1975).

An ethogram for *N. ursus* was essential for several reasons. *N. ursus* had a more scattered dispersion during their active period (darkness) than during their resting period (illumination) (Chapter 7). This diurnal spacing is unlikely to be a function of a lack of shelter as the study channel contained an abundance of hiding places (see Chapter 3) and a wide variety of plant and animal species. In the case of cryptic species, spacing out may be a function of predator pressure (Tinbergen *et al.*, 1967; Croze, 1970) at least in those instances where the predator hunts by searching image (L. Tinbergen, 1960). Crypsis requires not only specialisations of form, but also specialised supporting behaviours. For example, cryptic animals must correctly orient themselves with their background and must remain motionless (Edmunds, 1974). Consequently, it was important to investigate the individual behaviours shown by *N. ursus* during both the active and inactive phases.

It is also possible that the mask plays a more active role in avoiding or repelling predators. For example, the algal pieces may serve as a specialised form of autotomy, or the species comprising the mask may have properties which are noxious or toxic to the predator (see Chapter 1). Consequently, it was also important to investigate the repertoire of anti-predator behaviours shown by *N. ursus*.

The spacing out of conspecifics is generally thought to be accomplished by agonistic behaviours. 'Agonistic' is a collective term commonly applied to all those behaviours, ranging from threat and attack to defence and flight, which occur in conflicts between individuals in competition for resources (Scott & Fredericson, 1951; Hinde, 1970; McLay, 1981). Predatory conflicts were excluded from the concept of agonistic behaviour on the basis that during predatory encounters one contestant is the resource. Interspecific agonistic behaviour was not at issue in this study. Consequently, I have used the term 'agonistic' behaviour to refer solely to 'intraspecific agonistic' behaviour.

Overt fighting between animals not only carries the risk of damage and even death to one, or both, participants, but also incurs a large expense of energy, both of which lower an animal's 'fitness'. This reduced fitness can be regarded as the 'cost' to the animal (Caryl, 1979, 1981, 1982) and if an animal is to maintain its fitness the 'cost' of a given resource must not outweigh the benefit involved in acquiring it. Consequently, selection has acted on the individuals of many species, including the majority of crustacean species studied so far, to repel an opponent without resorting to physical combat. This has occurred by means of ritualised acts (Tinbergen, 1959; Blest, 1961) or displays.

In this thesis, Smith's (1968: p.41) definition of a display will be adopted:

> "... an output of an organism which has been selected and modified in the course of evolution to function efficiently as a social signal".

In turn, a 'signal' has been defined as:

> "... a small amount of energy or matter which induces a large change in the rate of energy release in a system" (Barnett, 1967)

and a 'social' signal as a signal produced by an animal and acting on a conspecific.

In the literature the term signalling is used interchangeably with 'communication'. Over the years the concept of communication has been applied in such a diversity of ways as to become almost meaningless (Klopfer & Hatch, 1961; Marler, 1961; Scott, 1964). For the purposes of this thesis I have adopted Barnett's (1967) definition and communication

is understood to mean "the process of inducing a change in another animal's behaviour". For a more extended discussion of the concept, see Molenock (1975).

'Displays' are motor acts which lack physical contact with the opponent, whilst 'fights' involve the physical interaction of opponents. 'Formalised' fights involve a "more or less fixed set of patterns following certain rules", whilst 'wild' fights involve an "irregular exchange of beats" which in Crustacea may occur "with or without grasping with the chelae" (Schone, 1968). In many animals the entire fight becomes a tournament, but in others, damaging fights occur but are ended by special inhibitory or 'submissive' displays. A submissive posture may be assumed by the loser following overt fighting or, following the establishment of a dominant relationship, by a subordinate crab when threatened by a dominant (Reese, 1962). Submission in crabs is generally portrayed by either flattening the ventral surface against the substrate or by ceasing to fight and rolling on to the back or side and making no further attempt at defence (Reese, 1962; Eibl-Eibesfeldt, 1967; Sinclair, 1977). In either case, the absence of motion by the submissive crabs appears to be critical (Reese, 1962; Edmunds, 1974).

Dominance/subordinance relationships are manifested through 'tension contacts' which are any encounter between two crabs in which one clearly retreats following a direct meeting (Bovbjerg, 1953; Lowe, 1956; Stevcic, 1971). The crab which causes the retreat, or mounts the other, is termed dominant. Conversely, the crab which in any particular meeting retreats or escapes or remains underneath is subordinate.

It has been hypothesised that the adventitious mask of *N. ursus* may have a signalling function in intraspecific behaviour (Chapter 1). Consequently, it was also important to investigate repertoire of agonistic behaviours shown by *N. ursus*. Before discussing this hypothesis, I must digress to consider the implications involved in the proposed signalling function of displays. In view of Dawkins' (1976) 'selfish gene' concept that basically an animal is a machine designed to preserve and propogate the genes that ride inside it, the best strategy for an individual to adopt in an agonistic encounter depends on what its opponent is doing (Maynard Smith & Price, 1973). It is better to be ambiguous about aggressiveness so the opponent cannot predict the 'cost' one is willing

to 'pay' (Maynard Smith, 1974). Further, Dawkins & Krebs (1978) contended that agonistic displays can be viewed as vehicles for the assessment of fighting ability. They also argued that although ambiguous about aggressive intentions, displays should provide reliable information about fighting ability. Since displays used in assessment are direct or indirect trials of strength, they involve the same cost to both participants and are consequently hard to bluff.

Accepting the hypothesis that displays allow assessment of fighting ability, the question arises: does the adventitious mask of *N. ursus* function in assessment? The construction and maintenance of the mask requires a large investment of time and energy, i.e., a large cost (see Chapter 5). In addition, it is possible that the mask may have a further 'cost' of causing excess drag during movement through the water, hampering locomotion and possibly lessening the chances of escape from predators. Consequently, only those animals which are the strongest can afford to 'waste' time in masking (see Zahavi, 1975) and thus masking would be hard to bluff. If this were the case, one would expect that only those crabs which displayed, masked, and vice versa. Hence, it is important to determine whether all classes of *N. ursus* display to all conspecifics.

The ideas of assessment and probing can also be applied to the analysis of courtship signals. For example, the mask may be used in mate selection of males by females: the 'fitness' of the male being assessed by some attribute of the mask applied. For example, female *N. ursus* may be attracted to males possessing the largest mask. Alternatively, strength or prowess may be assessed by the variety of algae applied. If the mask is used as an assessment cue in mate selection by females, one would expect some difference in the presence/absence or form of the mask between the different sex and maturity classes of *N. ursus*. Consequently, the ethogram must be determined for all classes of masked and unmasked *N. ursus* to determine any differences attributable to the mask, or to the sex, maturity or size of the crab.

A final important point remains to be considered. A stereotyped act can only truly be termed a signal if the occurrence of the motor pattern in time and space is such that, under natural conditions, it could usually be sensed by other animals, i.e., it must be a form of advertisement. Indeed, ritualisation is normally viewed as resulting

in the production of very conspicuous stereotyped acts (Cullen, 1966). As the mask comprises adventitious materials from the environment in which *N. ursus* makes every effort to remain (Chapter 7) the mask melds with its background whichever sense is used by the perceiver. In fact, when a masked *N. ursus* is in the intertidal area, it is inconspicuous to humans whether or not it is actually associated with a patch of algae. This lack of conspicuousness, to humans at least, suggests that the mask is unlikely to have a signalling function and, if it does, it will play, at most, a minor role. The apparently cryptic nature of the mask suggests that the mask may, in fact, impair an assessment of fighting ability, possibly resulting in escalated fighting. If the mask is an anti-predator deceit, and if it does also impair assessment between males resulting in harmful escalated fighting, then the predatory selection pressure must be intense to support such a handicap.

Many animal species use a series of graded signals (e.g., variations in the cheliped position in crabs: Schöne, 1968). Theoretically, the best way to win a resource with as little cost as possible is to start with a low bid and go higher only if necessary. The 'cost' could mean either an energetic cost of performing the display or more likely, the risk of retaliation with escalated fighting by the rival (Dawkins & Krebs, 1978). On this theme, it would be interesting to determine if *N. ursus* engage in more escalated fighting than in displaying and formalised fighting in comparison to non-masking crabs. If this is found to be the case, it would suggest that the mask does in fact impair assessment of fighting ability.

Size, which is generally physiologically linked with fighting ability, would be a good assessment cue. Studies have shown that in crabs size is effective in settling contests (Allee & Douglis, 1945; Cameron, 1966; Hazlett, 1966, 1968a;Hazlett & Bossert, 1966; Hughes, 1966; Rubenstein & Hazlett, 1974; Molenock, 1976). However, it is interesting to note that in the majid masking crab *Microphrys bicornutus* (Hazlett & Estabrook, 1974) and the pagurid *Pagurus marshi*, which bears accumulated detritus (Hazlett & Bossert, 1966), the adventitious material may in fact impair the assessment of size.

It is important to distinguish between assessment signals which give information and aggressive signals which enhance a posture, making

the display more conspicuous, and which are susceptible to bluff. It is possible that the mask may have an enhancement function making the display more conspicuous. For example, Hazlett (1972b) hypothesised that the algal mask of *Microphrys bicornutus* may serve to make the contrast between the striking pattern on the uncamouflaged cheliped surfaces and the rest of the cryptic crab even stronger. Theoretically, the mask may also highlight the agonistic display of *N. ursus* who also has strikingly marked unmasked chelipeds. Assuming that the mask does impair assessment, then this sudden contrast of colour patterning may also have an important function in intraspecific display. If this is the case, one would expect the contrasting colours of *N. ursus* to be emphasised during aggressive displays and concealed during submissive ones.

In order to react to a stimulus, an animal must first be able to perceive that stimulus. Consequently, in addition to determining an ethogram for *N. ursus*, it was important to gain a basic understanding of their perceptual abilities by determining:

(1) the sensory modalities used in agonistic and predatory encounters; and

(2) the stimuli perceived and at what intensities and from what distances.

8.2 METHODS

N. ursus were only active at night (Chapter 7) and, in the field, were only accessible for observation during low tides. The nine attempts to observe behaviour in the field (refer Chapter 7 for details) met with little success owing to poor visibility and/or to the effects of observer disturbance to the crab from water movements and torch light, even with the use of a red filter. However, *N. ursus* were found to react readily to stimuli in the laboratory, so their ethogram was determined largely by laboratory observations. The 32 *N. ursus* successfully observed in the field yielded 21 instances of resting behaviour, 17 of locomotory, 7 of feeding amongst *Corallina*, 2 of masking, 2 of displaying, 2 of excavating and 4 of withdrawal from conspecifics. As there were only a few field observations these were not dealt with separately, but in conjunction with the results from laboratory observations.

In deference to the nocturnal nature of *N. ursus* the following behaviour observations and preliminary experiments were conducted either during periods of natural darkness or with crabs which had had their activity cycle reversed, during conditions of induced darkness.

White light flashes of even short duration may have a significant effect on crustacean activity (Hindley & Penn, 1975). Hence, red light was chosen as a suitable form of illumination under which to study the behaviour of *N. ursus* as, although humans have comparatively good vision in the red end of the spectrum, the spectral sensitivity of the marine Crustacea investigated is extremely low at wavelengths above 600 nm (red) and their visual pigments cluster in the region of 500 nm (see Table 8.1). In addition, red light has been successfully used to study the behaviour of other Crustacea (Naylor, 1961; Bregazzi & Naylor, 1972a, b; Al-Adhub & Naylor, 1975).

During the extensive preliminary observations, every movement seen was noted. This method of observation is generally recognised as the best for preliminary behaviour work (Smith, 1968). The data were either immediately written down or, where possible, recorded verbally on a tape recorder for later transcription.

There are several ways of analysing data generated by this form of observation and recording (Nolan & Salmon, 1970; Sinclair, 1977). However, owing to the preliminary nature of this work, and the varying and often small number of animals observed under *identical* conditions for each of the various behaviours, the results were only analysed qualitatively, not quantitatively. Those behaviours which were deemed to be significant to the central aim of this thesis were investigated quantitatively in Chapters 7, 14 and 15.

8.2.1 Perceptual Abilities

The perceptual abilities of an animal are commonly tested by presenting various standard stimuli to the different classes of that species (e.g., males, females, juveniles, adults) in a constant stimulus situation (Hazlett, 1966, 1968a,b, 1969, 1970, 1972a; Nolan & Salmon, 1970; Teytaud, 1971; Sinclair, 1977). This procedure proved unsuccessful since it was impossible to confine the crabs in the same initial starting

Table 8.1 The maximum sensitivity values, in the dark adapted state, of the various Crustacea studied.

Species	Maxima (nm)	Reference
Euphausia pacifica	462	Kampa (1955)
Meganyctiphanes norvegica	462	Wald & Burg (1957)
Libinia emarginata	493	Wald (1968), Hays & Goldsmith (1969)
Palaemonetes vulgaris	496/555	Goldsmith & Fernandez (1968)
Eupagurus bernhardus	500	Stieve (1960)
Carcinus maenas	502-506	Bruno, Mote & Goldsmith (1978)
Callinectes sapidus	505	Goldsmith & Fernandez (1968)
Leptodora kindtii	510	Wolken (1971)
Orconectes virilis	510/562	Wald (1968), Goldsmith & Fernandez (1968)
Pleuronrodes planipes	523	Fernandez (1973)
Homarus americanus	515	Wald & Hubbard (1957), Waterman (1961)
	525	Kennedy & Bruno (1961)
Homarus vulgaris	525	Kampa, Abbott & Boden (1963)
Squilla manthis	535-555	Schiff (1963)
Palaemonetes paludosus	550-555	Goldsmith & Fernandez (1968)
Procambarus clarkii *	570	Kennedy & Bruno (1961), Wald (1968)

* Fresh water species

place and orientation without disturbing them and, consequently, altering their behaviour. In addition, it was difficult to present the stimulus to only one sensory modality. Consequently, the perceptual abilities were not studied exhaustively. Instead, as chance permitted, notes were kept of the reaction of *N. ursus* to various stimuli encountered during the course of all the studies presented in this thesis.

8.2.2 Individual Behaviours

There was no special technique involved in the observation of these behaviours. *N. ursus* were observed in their natural environment in the field and in the simulated natural conditions provided in the holding tanks and on the trays used in the experimental tank (refer Chapter 13 for details).

8.2.3 Intraspecific Agonistic Behaviour

The stimuli which elicited intraspecific behaviour were provided by live *N. ursus* which, although kept in an aquarium, were nevertheless free-ranging. Consequently, the number and type of stimuli presented to any particular crab, or within any observation period, varied. *N. ursus* were selected according to the presence/absence of the mask, sex, maturity, and size (large 30 - 39.9 mm; medium 25 - 29.9 mm, and small 20 - 24.9 mm). Prior to any observation period the appropriate crabs were introduced into separate compartments of a triple tank which was supplied with sea water from the circulating system, an air flow and one half of a *Mytilus* as food, and allowed to acclimate. No two *N. ursus* encountered each other in more than one observation session and they were selected from different holding tanks. This method controlled for the parameters of sex, reproductive phase, starvation, temperature, tidal movements, prior isolation, and previous wins, all of which are known to affect crustacean agonistic behaviour (Lowe, 1956; Crane, 1957, 1958; Allen, 1966; Hazlett, 1966; Warner, 1970; Courchesne & Barlow, 1971; Rubenstein & Hazlett, 1974; Sinclair, 1977; Thorp, 1978).

The observation tank was supplied with enough pea gravel to provide traction, but not enough to enable the crabs to bury themselves. Hiding places, which also affect agonistic behaviour (Lowe, 1956;

Cameron, 1966), were omitted from the test situation to:

(1) increase the probability of encounters between crabs;
(2) increase the ease of observation of the crabs; and
(3) prevent having to extricate, and hence disturb, the crabs.

The only noticeable artefact of this highly artificial, monotonous and confined environment was an inability of the crabs to withdraw completely from an opponent. In the 'natural' environments the majority of potential encounters never eventuated because of mutual avoidance or the withdrawal of one party.

An observation period began when the partitions separating the crabs were removed. Recording commenced when there was an observable change in the behaviour of one crab irrespective of the distance between two animals, or when two crabs made accidental contact. An observation period was terminated when the overt signals of mutual response between the crabs ceased for over 10 min. All that transpired between the crabs during the total observation period was termed an 'interaction'.

The behavioural descriptions of intraspecific agonistic behaviour which follow were derived from observation periods of 1 - 1.5 h duration, of groups of six adult males (two large, two medium, two small), six females (two large, two medium adults and two small juveniles), and mixed groups of a large, and a medium-sized adult, and one small juvenile, of each sex. Observations were conducted both in the photographic dark room of EPFS Kaikoura and in the aquarium room, University of Canterbury.

8.2.4 Interspecific Behaviours

As the behaviour of live potential predators was too difficult to control, and as their presence undoubtedly generated various different stimuli simultaneously, interspecific behaviours were mostly generated by mechanical devices. The stimuli were presented from the front, rear, side, and over the subjects which were either buried in the substrate, on the substrate and adjacent to shelter, or over two crab lengths from shelter. The stimuli presented fell into five classes: distal, small tactile, large tactile, chemotactile, and unbalancing.

(a) Distal stimuli

These were presented to gauge the effect of an approaching 'predator' and included:

(i) Red and white illumination. In the field, illumination was provided by an 'Hitachi' torch with a detachable red filter, while the laboratory white light was provided by the general room lighting and red by a desk lamp.

(ii) Shadow. This was provided by a human hand passing over or beside the aquaria.

(iii) Water disturbance. In the field, water disturbance was occasioned by human feet walking by and fish swimming past the crabs. In the laboratory, water disturbance was generated by tapping or knocking the aquaria sides and by stirring the water with a glass rod.

(b) Small tactile stimuli

The tip of a fine paint brush, metal spatula or thin glass rod was used to stimulate one to two hair tufts on the body or legs of *N. ursus*.

(c) Large tactile stimuli

A large tactile stimulus was provided by a glass rod:

(i) swept across the dorsum in an arc simultaneously contacting numerous hair tufts;

(ii) continually moved back and forth in front of, behind, or lateral to the crab;

(iii) with a cotton swab affixed to the end, being rubbed back and forth across the crab.

(d) Chemotactile stimuli

(i) Octopus swab. A cotton swab, affixed to the tip of a glass rod, was wiped along the suckers of an *Octopus maorum* tentacle and then rubbed over the crab's dorsal surface.

(ii) Dead octopus. A freshly killed small *Octopus maorum* was fixed to a glass rod and moved, tentacles first, over the crab.

(iii) Live octopus. A live *O. maorum* was introduced into an aquarium containing free-ranging *N. ursus*.

(iv) Live octopus tentacle. As the live octopus killed every *N. ursus* it captured it proved difficult to observe their behaviour. Consequently, the octopus was confined in a holding cage (Chapter 13) made with coarser mesh so that its tentacles could protrude through and reach *N. ursus* which were situated on gravel on a bucket lid. However, the octopus could not draw the captured crabs back through the mesh and was consequently forced to release them.

(e) Unbalancing

The crabs were flipped ventral side up, or turned so they lay on their sides, by a metal spatula, a glass rod or by human hand alone. Flipping by hand was often followed by enclosing the crab in the hand.

The type, duration, elicited response and subsequent behaviour for each presented stimulus was noted.

8.2.5 Filming

Ciné film, which is an invaluable tool for recording behaviour (Scott, 1968), was taken of the most important behavioural sequences.

Since extensive preliminary observations suggested that the agonistic repertoire of adult male *N. ursus* was greatest over the widest range of eliciting stimuli, the group used for filming consisted of four adult males, two large ones matched for size; a medium and a small one. Although an adult female and a juvenile male and female were also included in the group, the majority of the film recorded the behaviour of the adult males. As the preliminaries had revealed no difference in the responses emitted by masked and unmasked *N. ursus*, only crabs with little or no algal covering were used, making filming and frame-by-frame analysis easier.

The *N. ursus* were put into a triple tank, in the Zoology Department as described for the previous observations. However, no special lighting was used. The tank was situated near the window on a moonless night. Filming was accomplished using a Bolex H-16 reflex camera with a 25 mm TTH f 1.9 taking lens and an American 'Night Technology Zeniscope' (NiTec) image intensifier equipped with a Vivitor Series 1 70 mm - 210 mm Macro Zoom. The film was a mute 18 f.p.s. Fuji RT 400 normal colour film.

The films were analysed initially using the frame-by-frame facilities on the movie projector. However, when a frame was frozen, the projector light dimmed (to prevent overheating) making analysis extremely difficult. Consequently, the films were transferred to JVC video tape and analysed on a JVC video cassette recorder. The slight definition lost by this transformation was well compensated for by the ability to examine each frame at full illumination for as long as was required - an essential feature as colour film taken with an image intensifier becomes dichromatic green/white.

8.3 RESULTS

The following catalogue of motor patterns constitutes an ethogram for *N. ursus*. The patterns observed have been classified according to the major eliciting stimuli: no evident stimulation from another animal (Individual Behaviour), stimulation by a conspecific (Intraspecific Behaviour), and stimulation by a predator-like stimulus (Anti-predator Behaviour). Each behaviour pattern is described the first time it occurs, and subsequently mentioned by name only. The precise eliciting stimulus(i) for each motor pattern is also described where detected. Any differences attributable to the sex, maturity, size or presence of the algal mask are discussed where they occurred.

The body parts of *N. ursus* are shown in Fig. 8.1 and for reasons of brevity are referred to as labelled in that diagram. For example, the anterior-most pair of ambulatory legs is referred to as AL1 and the left one as L-AL1.

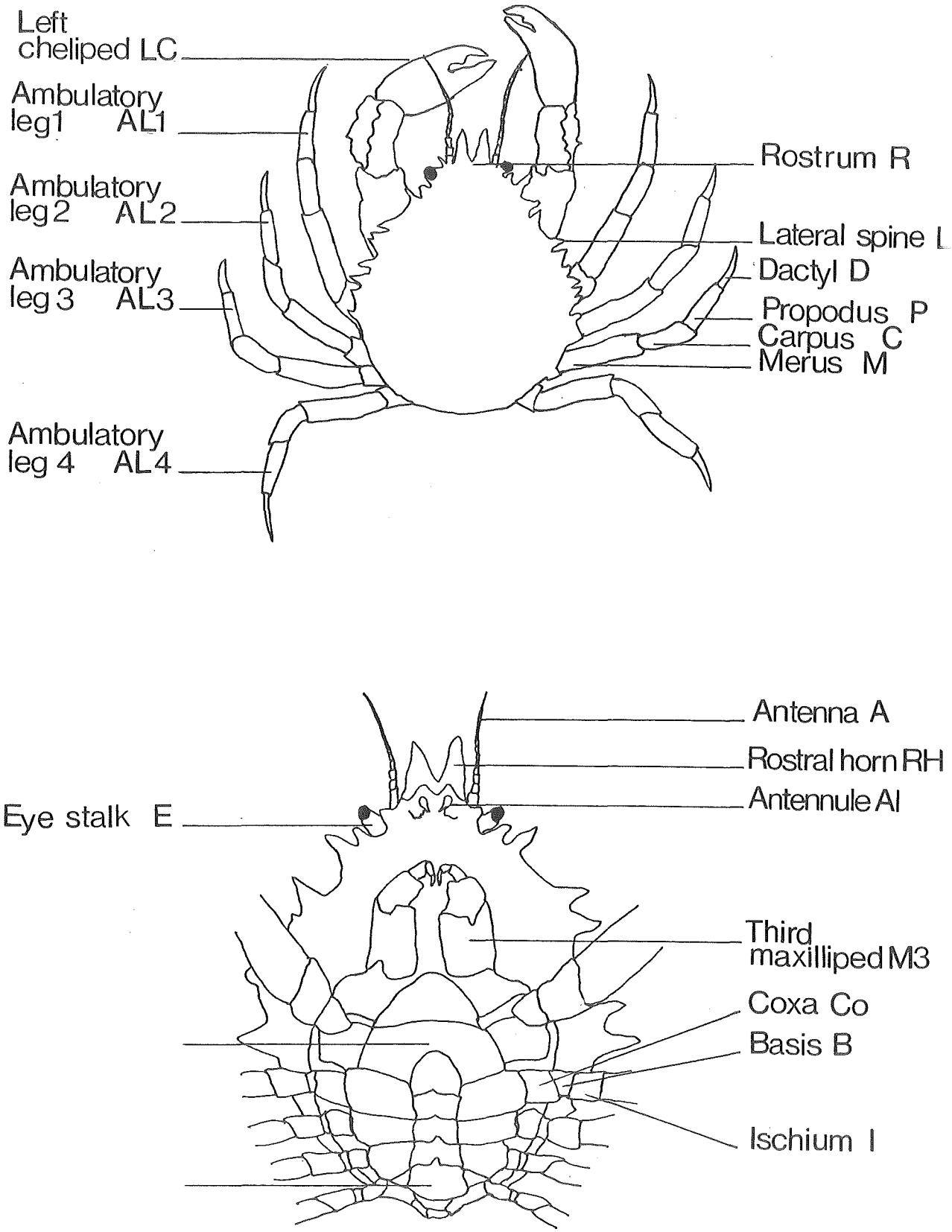


Fig. 8.1 Anatomical terms and abbreviations used to describe the behaviour of *Notomithrax ursus*. Top - dorsal aspect, bottom - ventral aspect.

8.3.1 Individual Behaviour

Resting position

When *N. ursus* was at rest on a horizontal surface the four pairs of walking legs were flexed at the carpus-merus (C-M) junction so that the dactyls were under the ventrum. As the anterior legs were longer than the posterior ones, this folding under of the ambulatory limbs resulted in the body being carried obliquely. The two chelipeds were also flexed at the C-M joint and held in such a way that they usually resembled inverted Vs (see Fig. 8.2)

Fig. 8.2 Characteristic resting attitude of *Notomithrax ursus* on a horizontal surface (hairs and adventitious mask not shown).

Sometimes the AL1 pair were stretched out on either side of the crab. The oblique angle of the longitudinal axis of the body was maintained by the partial flexion of the C-M joint so that carpus of the AL1 was at about 135° from the horizontal merus. This resting position was the same whether *N. ursus* were on top of the substrate or clinging beneath an overhanging rock or piece of laboratory equipment.

On vertical surfaces, particularly in grooves in the rock or aquarium walls, *N. ursus* adopted the same resting position as on a horizontal surface. However, they usually oriented so that the rostrum was directed towards the substrate. Whilst *N. ursus* were in the resting position, the antennules and mouthparts were frequently moved. Occasionally, a walking leg was flexed or a chela was raised to the mouthparts.

Stationary position

During short intervals between bouts of activity *N. ursus* became stationary with the longitudinal axis of the merus of each ambulatory leg parallel to the substrate and that of the carpus at approximately 45° to the substrate. The anterior of the body was lowered so that the rostral horns were parallel to the ground. The chelae were generally inverted as in the resting position. Occasionally, however, the crab stopped with the cheliped extended slightly anterior to the rostral area with the chela crossed, their tips resting on the ground.

N. ursus frequently became stationary against vertical surfaces including transparent glass. The posterior body together with AL2 - AL4 pairs rested against the substrate. AL1, and sometimes AL2, were extended rigidly to the left and right of the crab causing the whole ventral surface to press against the vertical surface. The chelipeds were again held in the inverted 'V' position.

Locomotion

All four pairs of ambulatory legs were involved in locomotion, while the chelipeds were held out of the way, generally in the inverted 'V' resting position. Movement was generally lateral to the anterior-posterior axis of the body. From the 'stationary' position this lateral movement was induced by flexion and then extension of the leading AL's and corresponding extension and flexion of the trailing legs.

Motion diagonal to, and also directly forward to, the antero-posterior axis of the body were also possible, but they did not occur as frequently as lateral motion. Backward motion was also exhibited, mainly when *N. ursus* was retreating from a stimulus or obstacle and was only maintained until the crab could move off laterally.

Generally, locomotion was unhurried, the crabs creeping along close to the surface. However, when subjected to adverse stimulation, such as bright white light, or the shadow or an observer, *N. ursus* were capable of rapid movement. In the field, one individual covered an open space of 25 cm in two seconds while another moved 15 cm in one second.

Climbing

The climbing of solid surfaces was achieved by forward locomotion in a vertical plane, coupled with an inward gripping action of the strong hooked dactyls. *N. ursus* were observed to climb rock, concrete, wood, rubber piping, and used perspex and plastic. The only substance seen to defeat these crabs was an expanse of glass wider than the diameter of the crab when its appendages were outstretched. Although perspex and smooth plastic initially defeated *N. ursus*, the dactyls rapidly scored the surface, enabling the crabs to take and maintain a hold.

N. ursus also climbed up into algal clumps in the same manner as used with solid surfaces. However, when moving over the tops of the clumps, these crabs used a lateral motion, swinging from frond to frond. The trailing legs would grasp the supporting frond, while the leading legs would extend until the dactyls could grasp a nearby frond. The trailing legs then released their frond and the leading legs flexed pulling the crab across the space between fronds.

Chela exploration

During bouts of locomotion, *N. ursus* often paused while one or both of the chelae probed under rocks or through the algal masses, picking and pushing at the material there. This behaviour was followed by further locomotion, excavating, or feeding behaviours.

The chelae were often employed to investigate objects right in front of the crab, seemingly being used instead of the eyes. For example, while masking *N. ursus* located the alga, directly in front of the rostral area and hence the eyes, by chela exploration as opposed to directly grasping the alga with the chela which one would expect if vision was being used. The same process was true of food location.

Shelter seeking

Under normal conditions both in the field and in the laboratory, *N. ursus* sought shelter during periods of illumination, either by excavating (Chapter 7) into the substrate or, more usually, by hiding in ready-made crevices in or under rocks or amongst algal clumps (Chapter 7). When deprived of cover in the laboratory, *N. ursus* would seek shelter

alongside dark contrasting objects such as the partition runners, or attempt to excavate.

During the active phase at night, *N. ursus* only sought shelter temporarily and, if undisturbed, rarely did more than create shallow depressions to rest in.

None of the *N. ursus* observed in the laboratory had any special resting places (territories). During periods of illumination they would remain almost motionless in one spot, but after dark they would move away to feed. When re-exposed to illumination they retired to a fresh place.

Scavenging

In the laboratory *N. ursus* readily fed on the freshly split *Mytilus edulis* provided. The chelae and AL1's were stabbed into the flesh, effectively pinning the *Mytilus* shell in one place, then the maxillipeds tore at the flesh, removing sizable pieces which were transferred to the mouth by chelae. This same scavenging behaviour was also observed in the field, the crabs using their chelae to tear off pieces from the detrital carrion. *N. ursus* were never observed to actively prey either in the laboratory or the field.

Grooming

Apart from the movements involved in the application and maintenance of the algal mask, *N. ursus* were only observed to engage in cleaning the eyes and, in gravid females, in cleaning the egg mass. To clean the eyes, the crab placed the endopodite of the third maxilliped over the orbital cavity, then the eye-stalks flipped up and the eyes were brushed. Gravid females were observed to continually lower the abdomen and systematically probe among the individual eggs (as in feeding), grasping foreign matter and flinging it away (as in excavating). This behaviour may also have served to help aerate the eggs.

8.3.2 Intraspecific Behaviour

(a) Reaction distance

During periods of inactivity such as darkness or when resting under

or by shelter during the active phase, *N. ursus* paid little evident attention to one another, often sitting with their legs entwined. However, during periods of activity their behaviour was markedly different and the following discussion will be concerned with these periods of activity.

If more than one *N. ursus* occupies a given area or space then, during the course of their active phase, there is a likelihood that one crab will approach the other. The outcome of an approach of one crab toward another is dependent on the direction of motion relative to the antero-posterior axis of both participants. For example, *N. ursus* are capable of lateral, forward and backward motion. Consequently, there are several types of positional relationships between two crabs. If more than two animals are involved, the positional relationships become more complex. Approaches between two *N. ursus* were most commonly front-to-front and in the following discussion this will be the case unless otherwise stated.

Bumping

Occasionally, contact between crabs was seemingly made accidentally with one animal backing or sidling into another. Bumping usually occurred if the active crab was fleeing or retreating from another stimulus. Reaction to a 'bump' depended upon the sex, maturity, and size both of the recipient and the 'bumper' as well as the direction of the bump.

Awareness

During approach, awareness of a conspecific occurred within five to six body lengths of one another. 'Awareness' was manifested by any change in the recipient crab's behaviour (e.g., avoidance, retreat or any of the agonistic behaviours [described below] which was directly attributable to the presence of the stimulus [other crab]).

Avoidance

Upon awareness of one another and providing there was no overt aggressive behaviour by either party and regardless of the positional relationship, the approaching crab would walk away from the other by

moving out of its path or detouring round it. *N. ursus* did not alter its 'locomotory' body position when avoiding another animal. Avoidance by either party terminated the interaction.

(b) Agonistic behaviour

If neither individual avoided the other, the interaction became more complex and a series of agonistic behaviours apparently of increasing intensity ensued.

The agonistic behaviours exhibited by *N. ursus* during an encounter with a conspecific (and another species) were combinations of acts selected from a basic pool of behaviours comprising movements involving the elevation and orientation of the body and positioning of the legs and chelipeds.

(i) Body elevation. Vertical movement of the body was effected by movements of the ambulatory legs (see Fig. 8.3).

Normal position

This is the 'stationary' position described previously.

Elevated position

The meri of the ambulatory legs were held nearly horizontal to the body and at right angles to the straight line of the carpus and propodus, raising the body high above the substrate. Even greater height was achieved by further adducting the dactyls.

Lowered position

The body was lowered close to the substrate by adducting the ambulatory legs under the body as in the "resting" position.

Extended lowered position

The legs were fully extended laterally so that the M-C-P-D formed a virtual straight line, horizontal and at right angles to the antero-posterior axis of the body.

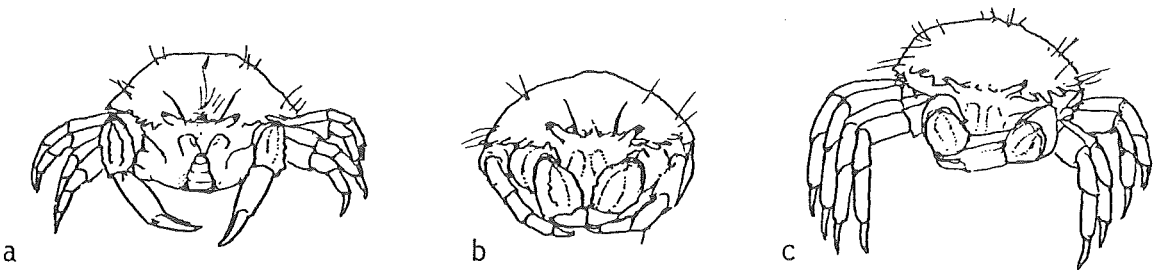


Fig. 8.3 Variation in body elevation of *Notomithrax ursus* during agonistic encounters (a - normal, b - lowered, c - raised).

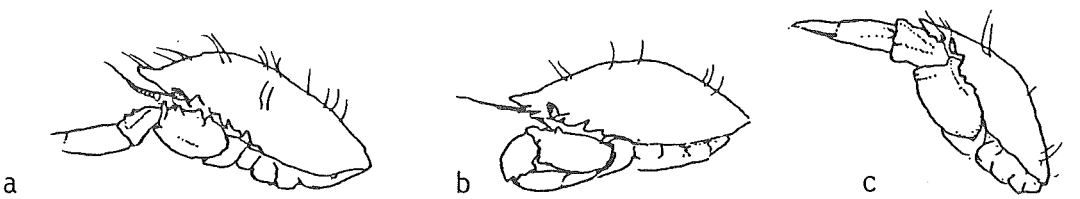


Fig. 8.4 Body orientation around a transverse axis (a - normal, b - forward, c - backward).

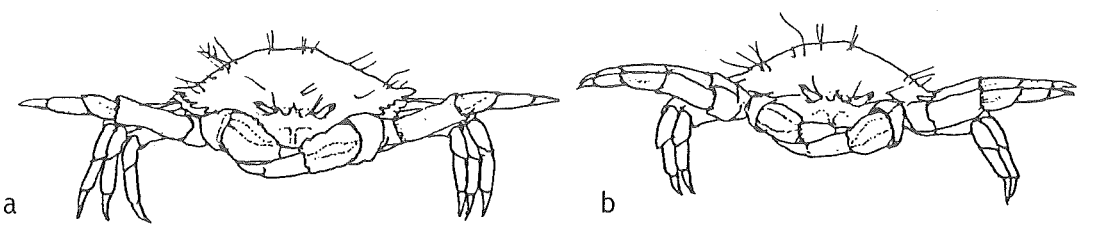


Fig. 8.5 'Raised parallel' leg position during agonistic interactions (a - first pair, b - first and second pair).

(ii) Body orientation. The body was rotated around the transverse axis so that more of the yellow-haired, algae covered dorsum or more of the red, white and bluish-grey ventrum and chelipeds were exposed (Fig. 8.4).

Normal

The body was carried obliquely; the antero-posterior axis was at an angle of approximately 20° - 25° to the substrate, with the anterior portion further from the substrate than the posterior portion, as in the "resting" and "locomotory" positions.

Rotated back

The body was rotated back 25° - 30° so that the posterior portion approached the ground and the antero-posterior axis was at an angle of about 45° - 55° to the substrate.

Rotated forward

The body was rotated forward so that the antero-posterior axis was horizontal with the substrate, exposing the dorsum to the opponent.

(iii) Leg position. As well as carrying the body, the AL's could be raised and held above the substrate either singly or in combinations of up to four legs at once from adjoining pairs (Fig. 8.5).

Raised parallel

The ambulatory leg was raised and extended so that M-C-P-D lay in a virtually straight line horizontal to the substrate and at an approximate 90° angle to the vertical body axis.

Raised arch

The merus of the ambulatory leg was adducted towards the dorsum so that it made about a 135° angle to the vertical body axis while the carpus and propodus are held in a straight line horizontal to the substrate.

(iv) Cheliped position. The chelipeds, individually or together, were moved to and held in one of four postures, recognised by the

experimenter, and achieved by a combination of spreading and elevating them. Movement was often occasioned by repeatedly repositioning the chelae (Fig. 8.6).

Adducted

The chelipeds were adducted under the ventrum in the "inverted V" of the "resting position".

Position I

The thoracic sternum - coxa joint (TS-C) was extended approximately 45° causing the chelipeds to lie slightly away from the body. The C-M joint was flexed until the carpus formed a straight line with the merus. The chelae were adducted into the A-P axis at the P-C joint so that their closed tips just met or were interlocked in front of the mouthparts.

Position II

The TS-C was adducted up towards the dorsum, raising the cheliped about 40° - 45° from Position I. The P-C joint was extended so that the chela pointed forward, its slightly parted tips forming a straight line with the longitudinal axis of the carpus. The C-M joint was flexed so that the carpus was perpendicular to the merus.

Position III

The TS-C joint was fully extended laterally so that the cheliped was perpendicular to the A-P body axis. Simultaneously the cheliped was raised by fully adducting the B-C joint towards the dorsum. In consequence, the chelae were held at the maximum possible distance from each other and their tips were fully opened.

The chelipeds served as weapons as well as organs of expression, being used to grasp or ward off an opponent as the occasion demanded.

(c) Aggressive acts

Aggressive acts were all those behaviours that served to halt the approach of another individual, or to cause them to withdraw. Vigorous combat was seen only when these aggressive acts failed to deter an opponent. Aggression commenced with the 'advance' of one crab toward another.

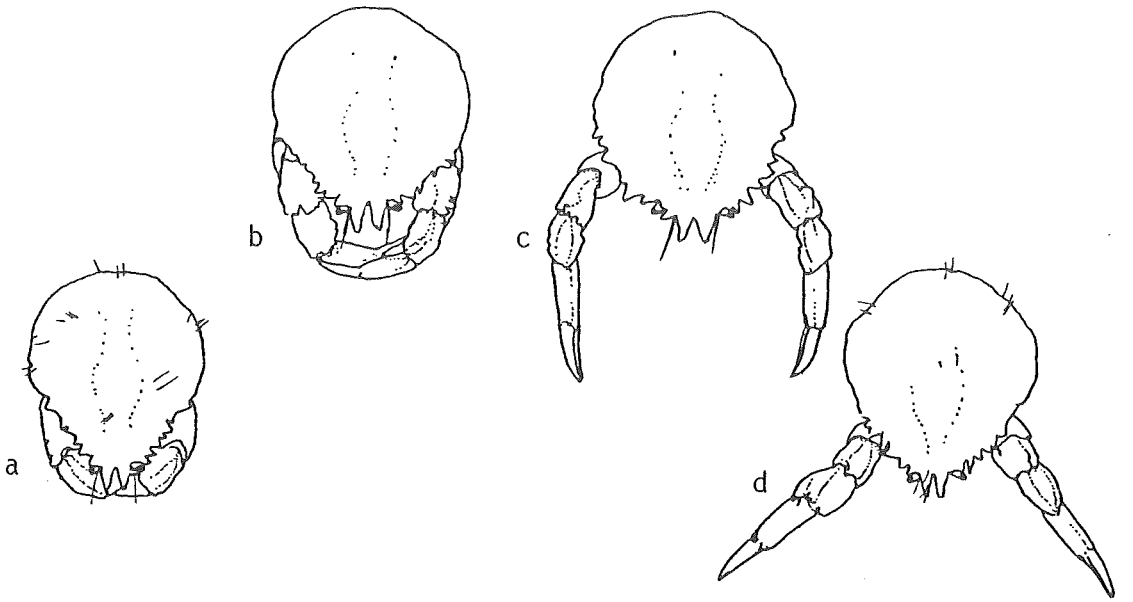


Fig. 8.6 Cheliped positions during agonistic interactions between adult males (a - neutral; b, c and d - low medium, and high intensity spreads).

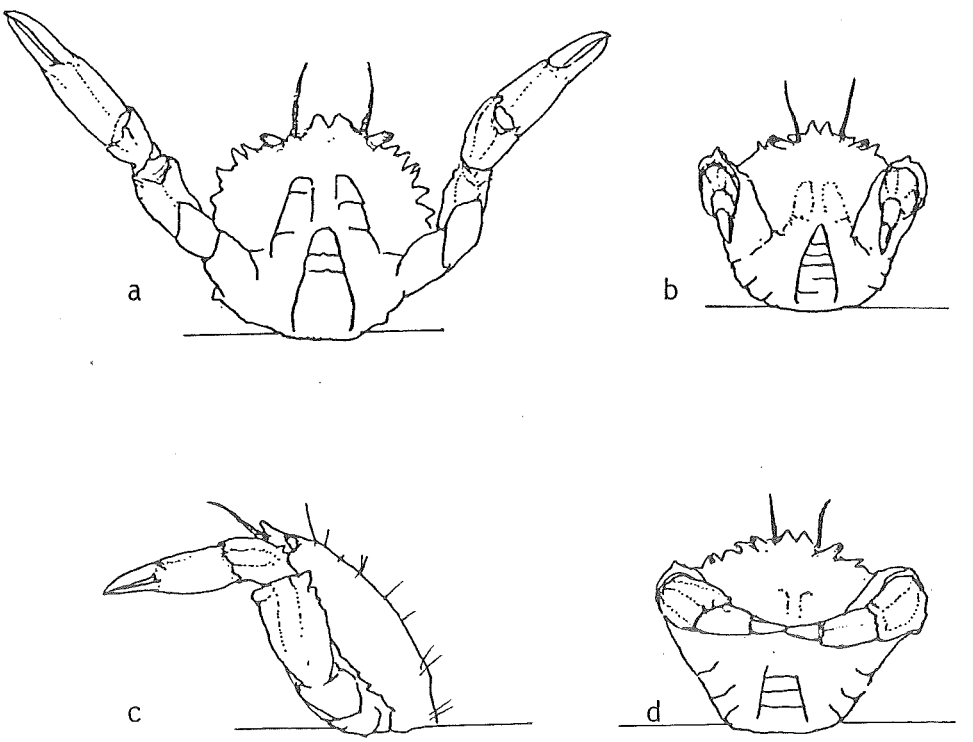


Fig. 8.7 Meral spread display of male *Notomithrax ursus* (a - high intensity, b and c medium intensity - anterior and lateral views, d - low intensity).

Advance

During general lateral locomotion the casual approach of one crab towards another changed to a direct frontal advance at approximately 3 - 5 crab lengths. The movement continued to be made sideways, and the change from approach to advance was marked by the abrupt elevation of the carapace (as previously described). The chelipeds were generally unflexed from their inverted 'V' resting position so that they became slightly posterior of perpendicular to the substrate.

Arch

The carapace was elevated and rotated backwards so that the anterior edge of the crab was raised above the opponent. This posture exhibited the red and white colouring of the adducted chelae, mouthparts and general ventrum and was an integral part of aggressive and active defensive behaviours.

Abdomen flapping

In the arched position the crab rapidly and repeatedly raised and lowered the abdomen. Although commonly observed in the brood care behaviour of females, this behaviour was also observed in males on four occasions. On three of these occasions the behaviour was exhibited on the introduction of a female (Chapter 6). On the fourth occasion, telson flapping was exhibited by a large adult male on being touched by a small adult male.

Bouncing

From the stationary position, the body was rapidly and repeatedly elevated and lowered, without rotation, by the flexion and extension of the ambulatory legs. This behaviour seemed to signal general excitation, being displayed by crabs adjacent to but not directly involved in an interaction between neighbouring crabs. Bouncing was often accompanied by random, rapid movements of the chelipeds and AL1's.

Meral spread (M-S)

The body was arched and the chelipeds were differentially spread and raised, exhibiting the chelae (weapons) and the contrasting markings on their external and then internal faces (Fig. 8.7). The meral spread posture was given as a prelude to contacting another crab, consequently

it has been considered a threatening behaviour. Alternatively, the M-S was a defensive reply to the aggressive behaviour of an opponent or predator. The intensity of the threat seemed to be reflected in the degree to which the chelae were separated, and three distinct forms of the M-S were evident.

M-SI - The chelipeds were extended to PI. In an initiating crab this position was rarely held for long being quickly followed by MSII or retreat by either party. During tapping, envelopment and chela grasping or pushing, the MSI position was maintained by the defensive crab until the aggressor ceased its behaviour. In defence, MSI appeared to protect the oral and rostral region from the adversary's chela blows.

M-SII - The chelipeds were extended to PII. This was the most common of the three postures and was exhibited to advancing, crouching or retreating opponents and after grasping an opponent.

M-SIII - The chelipeds were extended to PIII. This posture was usually exhibited before, immediately after, or during breaks in ritualised and, occasionally, wild, fights.

Movement of the chelipeds to the lateral merus posture was comparatively rapid (< 0.1 seconds). The chelipeds could be held in the lateral merus posture for many seconds before being either slowly lowered, being further extended if in the low or medium posture or changed to a contact behaviour.

Chela wave

From the high M-S position the crab closed the chelipeds to PI and then alternated between the three positions. The sequence and ratio of the three cheliped positions appeared random. For example, a wave consisted of: PIII - PI - PII - PI - PII - PI - PIII - PII - PIII - PI. Waving behaviour was given by one cheliped, or both in synchrony, and seemed to be an indication of intense aggression by the actor. Waving was exhibited when other behaviours had failed to repulse an opponent. For example, a large adult male began waving at a small adult male which it had failed to envelop and tip over. Another large adult male waved a single chela at its own reflection for over five minutes.

If the previous behaviours failed to repulse an opponent, then the initiating crab would either exhibit a submissive behaviour, retreat (see later) or engage in a contact behaviour.

Touching

Following a direct approach, the AL's of one crab were extended to touch and then move over a part, generally the AL's, of another crab. Touching, following a direct approach, was only observed among females and juvenile males. However, all *N. ursus* exhibited either touching or retreat following a bump with a conspecific. Touching was generally a slow movement and often seemed hesitant.

Chela probe

A crab slowly extended one, or both, cheliped in the direction of another crab until the chela tips made contact. The chela(e) was then probed around or moved slowly over the other crab. The slowness with which this action was carried out, and its similarity to 'chela exploration', suggests that this behaviour was of an exploratory nature. For example, a medium female crab chela probed a small female who had just touched her.

Tapping

The tip of the chela of the arched initiator was rhythmically and repeatedly brought into contact with the dorsal surface of the conspecific. Usually, taps were delivered by one chela only, at a rate of one to two/second, while the other chela was deployed in another activity such as hair grasping. However, sometimes both chelae, simultaneously or alternately, were tapped on a conspecific.

Envelopment

The chelipeds of an arched crab were moved either singly or together from PII to partially or totally embrace a conspecific in the 'crouched' or 'freeze' posture (Fig. 8.8). Usually the inner faces of the chelae and carpi of the chelipeds of the enveloping crab contacted the enveloped crab's carapace. Occasionally, considerable force was applied when the chelipeds of the enveloping crab were spread laterally and then rapidly moved together to strike the enveloped crab. One large adult male was observed to attempt to envelop three smaller males - a feat it did not accomplish.

Chela grasp

The cheliped of an arched crab was extended and the chela tips

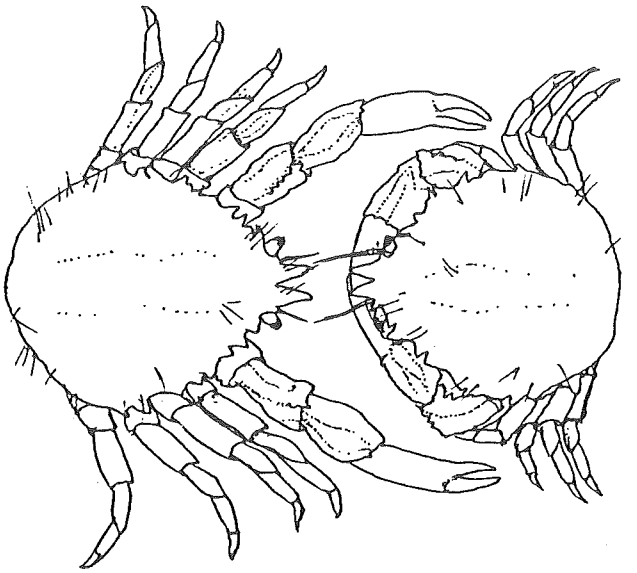


Fig. 8.8 Envelopment during an agonistic encounter between adult male *Notomithrax ursus*.

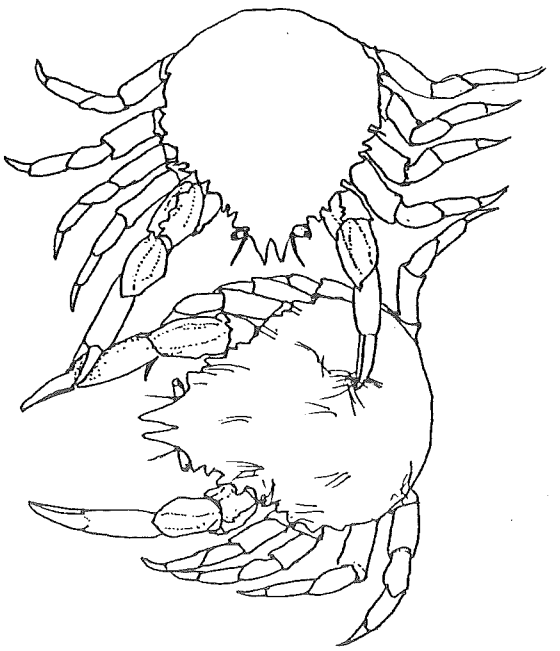


Fig. 8.9 Grasping between adult males.

grasped the adversary (Fig. 8.9). Generally the grasping crab held the conspecific's dorsal surface, particularly the hair tufts and, where present, their associated algal pieces. Grasping of the orbital area and cheliped and ambulatory leg joints was also common. However, any part of the opponent was liable to be grasped. Generally both chelae were used and they grasped different parts of the opponent. Chela grasping was often a prelude to fighting or, alternatively, elicited flight by the crab which was grasped. Pressure great enough to cause visible injury to the grasped individual was not observed.

Chela push

The arched crab forcefully extended the cheliped and used the tip (PIII) or external face (PI) of its chela to push against the opponent's claw or, less frequently, against the front edge of its cephalothorax, pushing the adversary from its space. Pushing was always directed frontally to the opponent and one or both chelipeds were involved. Leverage during pushing was afforded by digging the AL3 and AL4 pairs into the substrate or bracing them against a vertical surface where possible. Frequently the two crabs involved attempted to lock chelae.

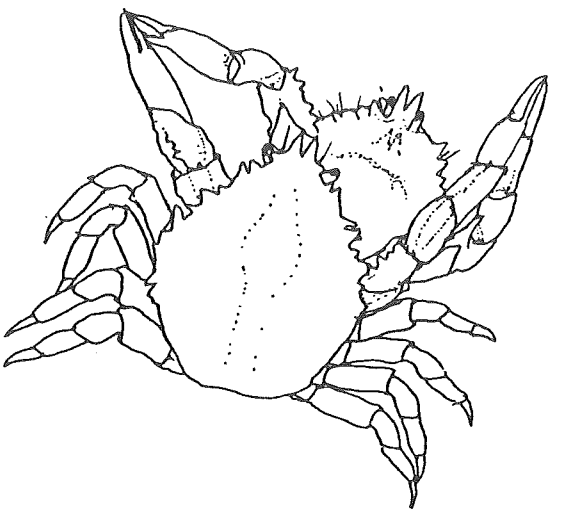
Chela strike

The cheliped was rapidly moved to PIII and where necessary the body was oriented front-to-front with the opponent. The chela was then rapidly struck against the opponent and the cheliped was quickly withdrawn. As the opponent generally struck back or parried the blow by holding its chelipeds in PI, chela strikes generally were to the opponent's chelipeds. Often the strike was repeated two or three times.

Formalised fight

This behaviour was similar to chela pushing. Both crabs 'advanced', the chela in PII. Occasionally they would strike at one another. When close to touching, both crabs spread their chelipeds to PIII and then moved together so that the chelipeds met along the length of their inner faces (Fig. 8.10). Frequently they also locked their chelae tips. This posture lasted for several seconds, during which time both individuals pushed against each other. The pair remained

a



b

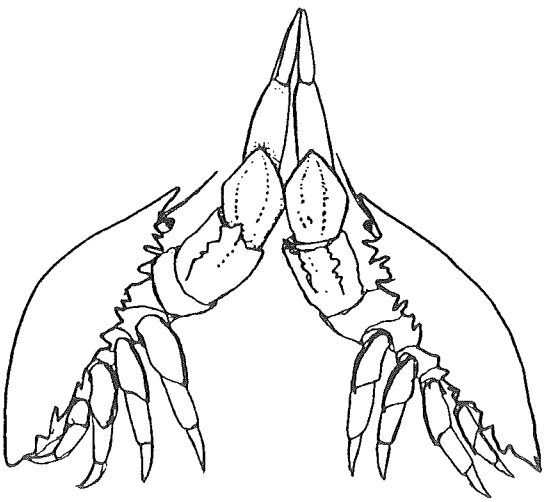


Fig. 8.10 Formalised fight between adult male *Notomithrax ursus*. a - frontal view of crabs coming into position; b - lateral view of final posture.

stationary if both pushed simultaneously, and moved back and forth if they pushed alternately. On one occasion the crabs were observed to retreat slightly and then to bring their chelipeds rapidly together medially and down, so that their chelipeds hit together.

This behaviour was only observed between adult males well matched for size, and even then it was rare.

Wild fight

This was an unstereotyped encounter, consisting of rapidly repeated, sometimes reciprocal, strikes interspersed with pushing, envelopment and grasping of the opponent's hair tufts and limbs. Sometimes more than two adult males participated and both the chelae and AL1's were involved resulting in a seemingly tangled mass of limbs. The rapidity and violence of the actions and the tangled mass of the numerous limbs involved made a more accurate description of these wild fights impossible, even using frame by frame analysis. One obvious recurring feature was the attempt to twist an opponent's limbs at a joint. This 'twisting' never resulted in any damage to either participant during the wild fights observed in the laboratory. However, previously healthy adult males in the laboratory were often found to have suffered broken or missing chelae, and occasionally chelipeds, suggesting that harm could be inflicted. These wild fights were frequent among adult males of both approximately equal and relatively differing sizes and often lasted for several minutes. One fight between a large, and a small, adult male was timed at just over five minutes.

Tipping

During a wild fight the larger participant impeded the flight of its adversary by grasping the other crab, particularly by the cheliped or hair tufts. At this point the 'grasped' crab often shoved and grasped the imprisoning claw and, if it managed to free itself, would flee. Meanwhile the aggressor would attempt to tip the other crab over by inserting the inner face of its free cheliped under one side of the imprisoned opponent's ventrum and then raising the straightened cheliped up and in towards the midline. As the other chela was pinning the opposite side of the opponent down, the imprisoned adversary was effectively rolled sideways toward the imprisoning chela. The

imprisoned crabs were never observed to be rolled completely on to their dorsum and this may have been an artefact of the smallness of the observation aquaria, as generally the rolling crabs ended up against a neighbouring conspecific or a glass wall. On one occasion a large adult male successfully flipped a medium adult male forward on to its rostral area but the crab teetered and then regained its equilibrium.

(d) Defensive acts

Aggression from a conspecific elicited one of three types of reaction in an adversary: retaliation behaviours, immobilisation and withdrawal. The first type of behaviour exhibited was defensive while the other two categories, which are characterised by a lowering of the body and adducting the chelipeds, effectively concealing the weapons and ventral patterns, can be considered submissive.

(i) Retaliation. *N. ursus* retaliated by using one of several behaviours depending on which was appropriate to the situation. The behaviours involved in wild and ritualised fights have already been discussed.

Cheliped shove

This was a highly variable behaviour which had the common element of rapidly thrusting a cheliped in the direction of a conspecific. If the cheliped actually made contact, the adversary was forcefully repulsed. The cheliped shove differed from a cheliped strike in several ways:

(1) shoving was occasioned whichever part of the cheliped made contact and involved a pushing action not a striking one;

(2) the cheliped was directed at the stimulus rather than being held in a certain position relative to the body and then orienting the body towards the stimulus;

(3) a shove was elicited by an accidental contact between two animals who had not immediately previously been engaged in an encounter;

(4) a shove was not preceded or followed by other aggressive acts on the part of the exhibitor. The encounter was terminated on the repulsion of the recipient crab;

(5) shoving elicited withdrawal behaviour, usually retreat, from the recipient;

(6) shoving was exhibited by adult females and young as well as adult males.

The cheliped shove appeared to function only to rid the exhibitor of an adverse stimulus — the encroachment of space by a conspecific.

Chela pinch

This behaviour appears to be a more intense form of the cheliped shove, involving all the movements of a shove except that it culminated in the pinching of the contacted area of the adversary between the chela tips. The cheliped was held in PII, not PIII. Chela pinching differed from grasping in that the pinch was momentary and no attempt was made to continue the chela hold nor to lock chelae with the antagonist. However, pinching occasionally resulted in momentary hair grasping. In turn, the force of the pinching cheliped sometimes caused the momentarily held crab to be swung away. Adult males were never observed to exhibit this behaviour, but it was the most intense and most common form of retaliation exhibited by females and juvenile males.

Kicking

Kicking consisted of short, jerking movements of the carpus of each AL, caused by repeated flexion and extension of the carpus-merus joint. During kicking the body was elevated slightly and the chelipeds were adducted. Kicking was always elicited by a conspecific stroking or tapping the ambulatory legs concerned. It was also given in response to grasping, dorsal tapping and envelopment by an adversary.

Low M-SI

The body was lowered and the chelipeds were extended to PI. This reaction was exhibited by adult males and was a response to chela strikes and chela pushing by an adult male adversary or to body contact by any conspecific.

Meral-Spread

The frontal advance of an adult male exhibiting a meral-spread

elicited a reciprocal meral-spread (as previously described) in an adult male recipient and immobilisation or withdrawal by adult females and juveniles.

Reverse meral-spread

When contacted between AL4's by a conspecific, *N. ursus* gave a meral-spread. This behaviour differed from the other M-S displays by orientation to the stimulus rather than posture: the chelipeds faced away from the eliciting crab. Again, the spread of the chelipeds appeared correlated with the strength of the (rear) stimulation. At most, the reverse meral-spread elicited touching of the 'defender' by the dactyls of the outstretched AL's of the conspecific before one or both participants withdrew.

Pereiopod parallel

The chelipeds were adducted and the front of the body was lowered and rotated forward. The AL4's were then extended and raised straight out from the body, parallel to the substrate, and held in this position from one to over ten seconds before being lowered. This posture was only seen in encounters between adult males and was given in response to a MSIII exhibited by an adversary. This behaviour preceded the pereiopod arch and retreat behaviours.

Pereiopod arch

From the parallel position the AL's were adducted towards the dorsum (Fig. 8.11). The legs were either held briefly in this position before being lowered or they remained arched while the exhibitor backed off from the opponent in the MSIII posture. The combination of AL4 arch and retreat behaviours terminated the encounter. However, the exhibition of the AL4 arch only, by a small adult male, elicited a tipping attempt by its larger adult male adversary.

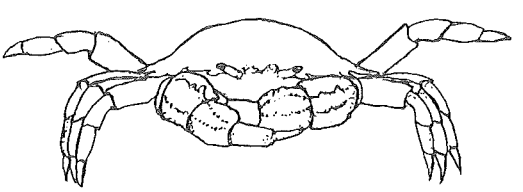


Fig. 8.11 Pereiopod arch by male *Notomithrax ursus*.

(ii) Immobilisation. Immobilisation was characterised by a lack of visible movement of the body and appendages. Only one form of immobile behaviour, the crouch, was displayed to conspecifics.

Crouch

The fingers of the chelae were closed and the chelipeds and legs were adducted under the ventrum. The body was rotated forwards and lowered. This behaviour was exhibited prior to contact by a threatening crab and consequently can be considered a submissive posture.

Crouching was exhibited by adult males who had lost an agonistic encounter with another adult male and by females and juvenile males in response to aggression by adult males. Crouching lasted from only a few seconds up to ten minutes and ended with retreat by the exhibitor. The duration of crouching was dependent on when the exhibitor was able to retreat.

(iii) Withdrawal. Withdrawal was the movement of one crab away from another conspecific after an encounter had been initiated by one and generally reciprocated by the other. Withdrawal consisted of two forms which differed by their orientation and speed. During both forms the body was rarely elevated, it was rotated forward and the chelae were usually adducted under the mouthparts.

Retreat

Retreat was the withdrawal of one crab from another by walking, at a normal speed, in the reverse direction from that crab, without changing the orientation of the body to the stimulus. Accidental physical contact (bump) to the side or rear, usually by the ambulatory legs, resulted in single or mutual retreat by any type of *N. ursus*. Retreat was also elicited by threat and/or direct physical contact by an adult male.

Flight

Flight was the withdrawal of one crab from another by running at an angle of 90° to 180° from its adversary. Flight was exhibited by adult males after losing a fight or in all classes of *N. ursus* after having the anterior of their body touched by an adult male.

(e) The effect of sex and maturity

The awareness of a conspecific was the same for all classes. However, there were marked differences between the responses of adult male *N. ursus*, and the females and juvenile males. These differences are clearly shown in the flow charts presented in Figs. 8.12 and 8.13. These flow charts are an amalgamation of sequences derived from the frame-by-frame analysis of ciné films of intraspecific encounters. Not all the behaviours were observed in any given encounter and frequently, because of the continuous nature of the stimulation, the behaviour sequences were cyclic.

Adult males exhibited all the aggressive acts listed except direct 'touching' and all defensive behaviours except chela pinching. The aggressive non-contact behaviours from advance through to MSII and the contact behaviour chela probe were exhibited to all conspecifics. The remaining aggressive acts were only elicited by other adult males. The defensive behaviours of kicking and reverse M-S were elicited by contact with all conspecifics while the remainder of the defensive behaviours were only elicited by adult males.

The responses of females and juvenile males were identical. The most frequently observed behaviour with these crabs was avoidance of a conspecific, particularly adult males. When challenged by adult males, females and juvenile males exhibited crouching and withdrawal behaviours. The only aggressive behaviours shown were direct touching and chela probe. Both of these behaviours were preceded by advance and arching and they were elicited by all except adult males. In active defence, females and juvenile males exhibited the cheliped shove, chela pinch and pereiopod kicking to other females and juvenile males. Contact of the body between the AL4's elicited a reverse MSII or flight.

(f) The effect of size

There was no noticeable size-related behaviours among females and juvenile males. However, among adult males there was a marked size difference in the behaviours elicited by the same and different sized adult males. In general, smaller male crabs retreated from larger male crabs. When fleeing, smaller male crabs were frequently observed to climb walls and even launch up into the water to avoid a larger male in its path. Larger male crabs chela shoved or grasped smaller male crabs

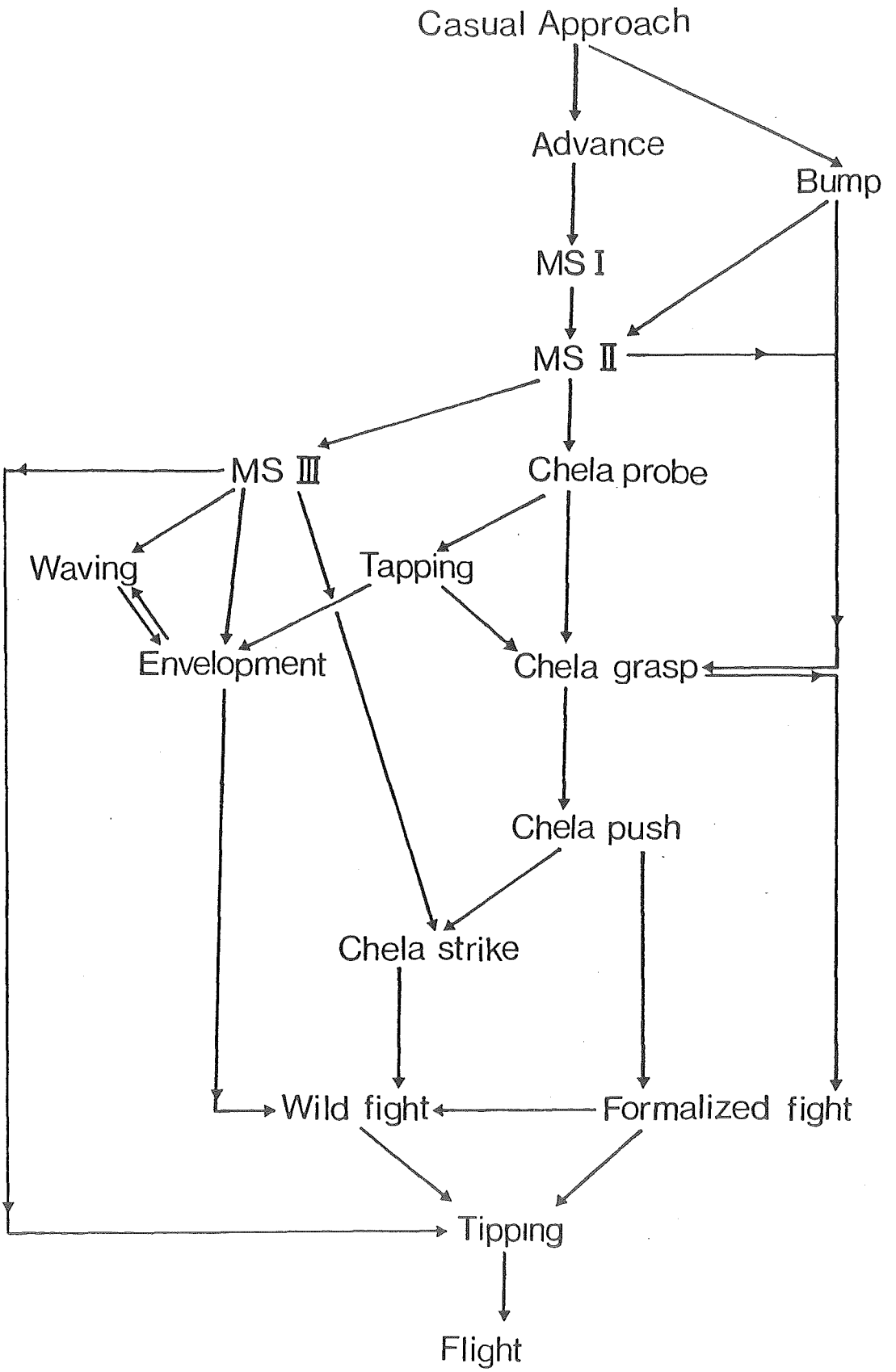


Fig. 8.12 Flow diagram of possible aggressive sequences between adult male *Notomithrax ursus*. Interactions can be terminated at any stage, after casual approach and prior to fighting by the retreat of one crab.

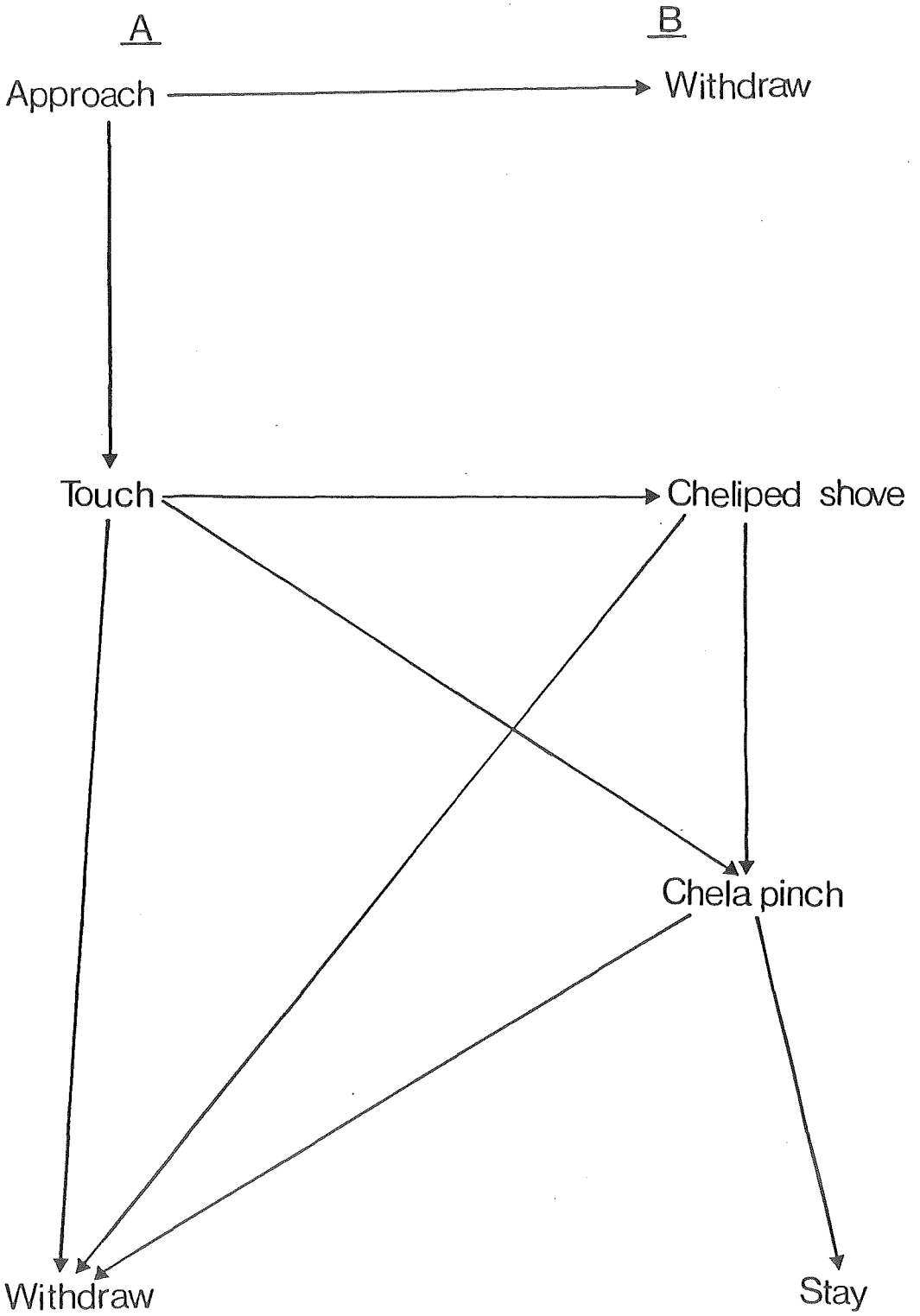


Fig. 8.13 Flow diagram of possible aggressive sequences between female and juvenile male *Notomithrax ursus*.

which approached them. The exception to this was recently moulted crabs which avoided all aggressive behaviour with other adult males.

If unable to escape, smaller adult males would retaliate against larger males resulting in wild fights. (Inability to escape was undoubtedly an artefact of the small observation tank.) Disputes between crabs well matched in size generally resulted in either formalised or wild fighting, the latter often eventuating from the former.

(g) The effect of approach direction

(i) Approached from the rear. Contact of the body between the AL4's, by any conspecific, elicited withdrawal in all *N. ursus*. Continual rear stimulation by a conspecific elicited a reverse MSII in females and juvenile males and a reverse MSIII or excavation in adult males.

(ii) Approached from the side. Stimulation to the legs by any conspecific elicited kicking and then flight in all *N. ursus*. 'Bouncing' was elicited in adult males which were lateral to a struggle or fight between other adult males.

(h) The effect of accidental contact

Adult males bumped frontally by females and juvenile males withdrew as did the 'bumping' crabs. Adult males bumped frontally by other adult males withdrew if the adversary was larger, cheliped shoved if the crab was approximately the same size, and chela grasped if the crab was smaller. Females and juvenile males fled when bumped frontally by adult males. When females and juvenile males bumped each other frontally, they either remained as they were, cheliped shoved, chela pinched, or withdrew.

Accidental contacts from the side or rear have been discussed above.

(i) The effect of the algal mask

There were no detectable differences in the behaviours exhibited by or elicited from masked and unmasked *N. ursus* regardless of the sex, maturity and size of the individual, and the orientation of the stimulus.

8.3.3 Anti-Predator Behaviour

Reactions to 'predator-like' stimuli varied according to the stimuli concerned, and many behaviours were the same as those elicited by threat or aggression by a conspecific. Consequently, the 'anti-predator' behaviours observed will be discussed according to the eliciting stimuli. Unless specified, neither the direction of approach of the stimuli nor the situation of the crab relative to shelter and the substrate changed the response elicited. Those behaviours unique to the anti-predatory repertoire are described on the first occasion they occur.

(a) Distal stimuli

(i) Light. The application of a beam of white or red light directly on to *N. ursus* in the field and laboratory elicited 'freeze' behaviour.

Freeze behaviour

This involved a variety of positions but it was characterised by an immediate cessation of the current activity, a lowering and forward rotation of the body so that the crab was pressed hard against the substratum, and by a tetanus of the appendages which were held as in the preceding occupation.

Gripping

If already in a crevice or under an overhanging object *N. ursus* clung tightly against the surface with the hooked dactyls and resisted strongly any attempt to move it from side to side or to pull it away from the rock. This gripping behaviour was particularly effective in their natural habitat and the only possible way for a human to dislodge an *N. ursus* in a crevice was to stimulate the body area between the AL4 pair. This stimulation resulted in the crab moving rapidly forward which had the effect of dislodging it.

Freezing and gripping behaviour were exhibited regardless of the sex, maturity, size or possession of a mask of the individual and was maintained for as long as several minutes.

The application of light in the general direction or vicinity of an exposed *N. ursus* elicited flight behaviour if the light was white, or momentary freezing and then resumption of the previous activity, or retreat, if the light was red. Withdrawal, whether flight or retreat, resulted in hiding behaviour.

Hiding behaviour

Hiding was exhibited by all *N. ursus* and included any behaviour which resulted in *N. ursus* being enclosed in available shelter, (e.g., overhanging rock, crevice, algal clumps [c.f. excavating behaviour]).

(ii) Shadow. When exposed to an overhead shadow *N. ursus*, both in the field and in the laboratory, froze if in an exposed space and hid if within one to two crab lengths from cover.

(iii) Water disturbance. Water disturbance, whether by human limb, a fish, or tapping of the aquaria walls, elicited hiding behaviour or freezing where cover was unavailable. Female and juvenile *N. ursus* in the laboratory were especially responsive to water disturbance.

(b) Tactile stimuli

(i) Small tactile stimuli. If *N. ursus* was buried or hidden, stimulation to one or two hair tufts by a paint brush, metal spatula or fine glass rod elicited freezing. Alternately, if *N. ursus* was exposed, stimulation to the dorsum elicited flight. Stimulation to the propodus and/or carpus of the ALs elicited kicking while stimulation to the merus of the ALs, especially AL1, elicited a reflex pinching action of AL1.

AL1 pinch

The meri of both AL1's are rapidly adducted towards the dorsum and the M-C joints are extended so that their carpi lie parallel to the substrate. This action traps the stimulus between the merus and the sharp protruding posterolateral spines which are driven into the stimulus. If the crab is grasped in the fingers this pinching produces a sharp pricking sensation.

(ii) Large tactile stimuli

Bent glass rod across the dorsum. Passing the rod in a slow sweeping arc across the dorsum always elicited freezing if the crabs were buried. However, if *N. ursus* were exposed, they fled, froze or excavated in a very unpredictable manner. The exhibition of these behaviours was not attributable to sex, size, maturity, time of daily cycle, nor presence of the mask.

Masked *N. ursus* were most sensitive to stimulation of the hair tufts, less so to stimulation of the algal mask and even less to stimulation immediately above the mask.

Continuous stimulation with bent glass rod. The behaviours elicited by continuous stimulation with a bent glass rod to the rostral area, the posterior (caudal) area between the AL4's and to the side of adult male *N. ursus* are shown in Figs. 8.14, 8.15 and 8.16. These flow charts are an amalgamation of sequences derived from the frame-by-frame analysis of ciné films of the stimulation of six adult males. Not all the behaviours were observed in any given encounter and frequently, because of the continuous nature of the stimulation, the behaviour sequences were cyclic not linear.

The 'anti-predator' behaviours exhibited by frontal stimulation were virtually the same as those elicited by a conspecific adult male with the addition of two unique behaviours: 'rocking' and 'bounding'.

Rocking behaviour

From the stationary position the crab rotated forwards and backwards around the transverse axis, pivoting on the AL4 and occasionally AL4 and AL3 pairs. Rocking was a prelude to chela strike and excavating (which, it is interesting to note, involved a sideways rocking around the longitudinal axis as the crab buried itself). Rocking was also exhibited during M-SII and M-SIII and when the crab was retreating. If exhibited during retreat, rocking was continued for several minutes after the crab had come to rest and the stimulus had long since ceased.

Bounding behaviour

Under extreme provocation, such as persistent prodding with a glass rod, flight occurred in a series of forward bounds in the direction

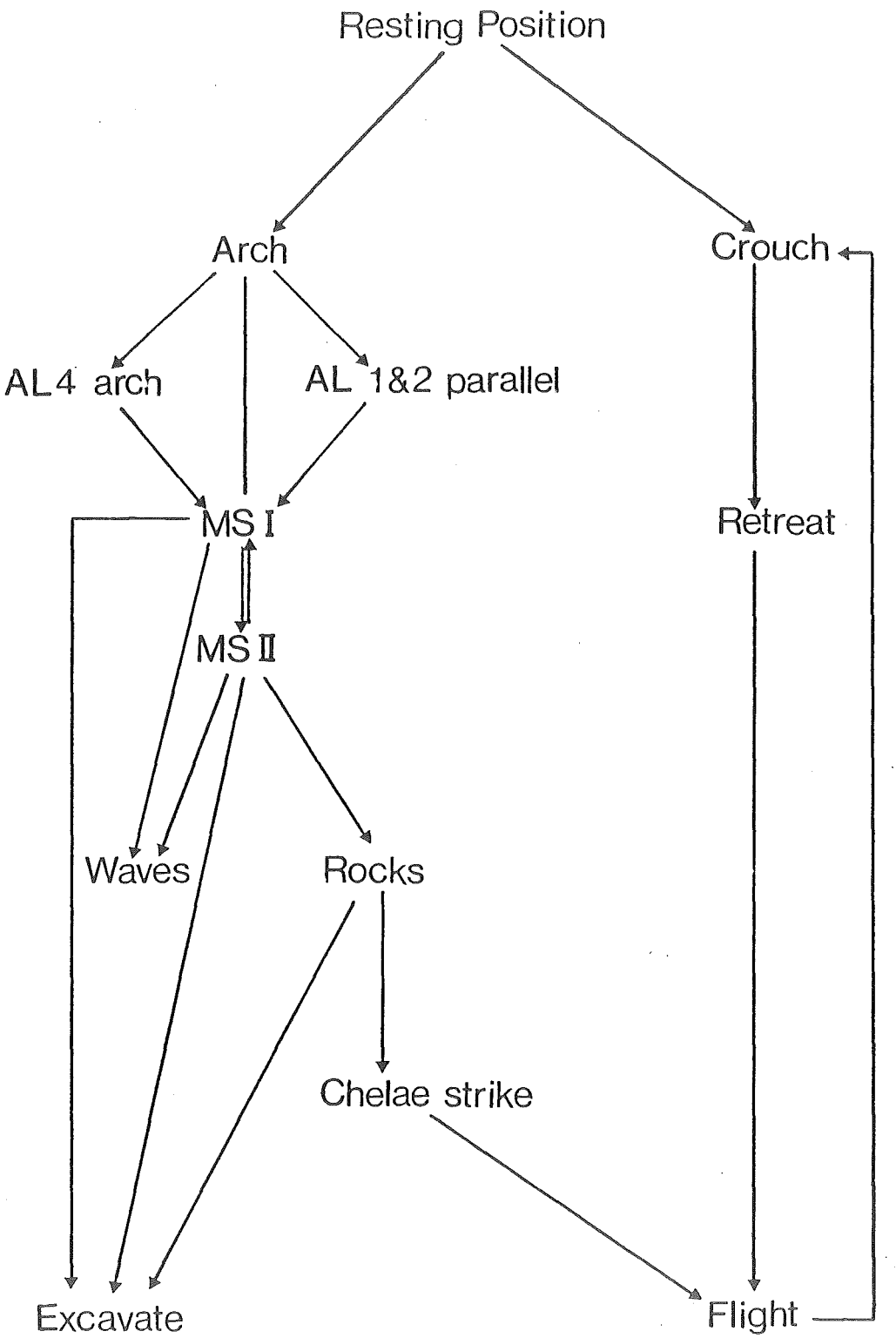


Fig. 8.14 Flow diagram of possible behaviours elicited by stimulating the front of an adult male *Notomithrax ursus* with a glass rod.

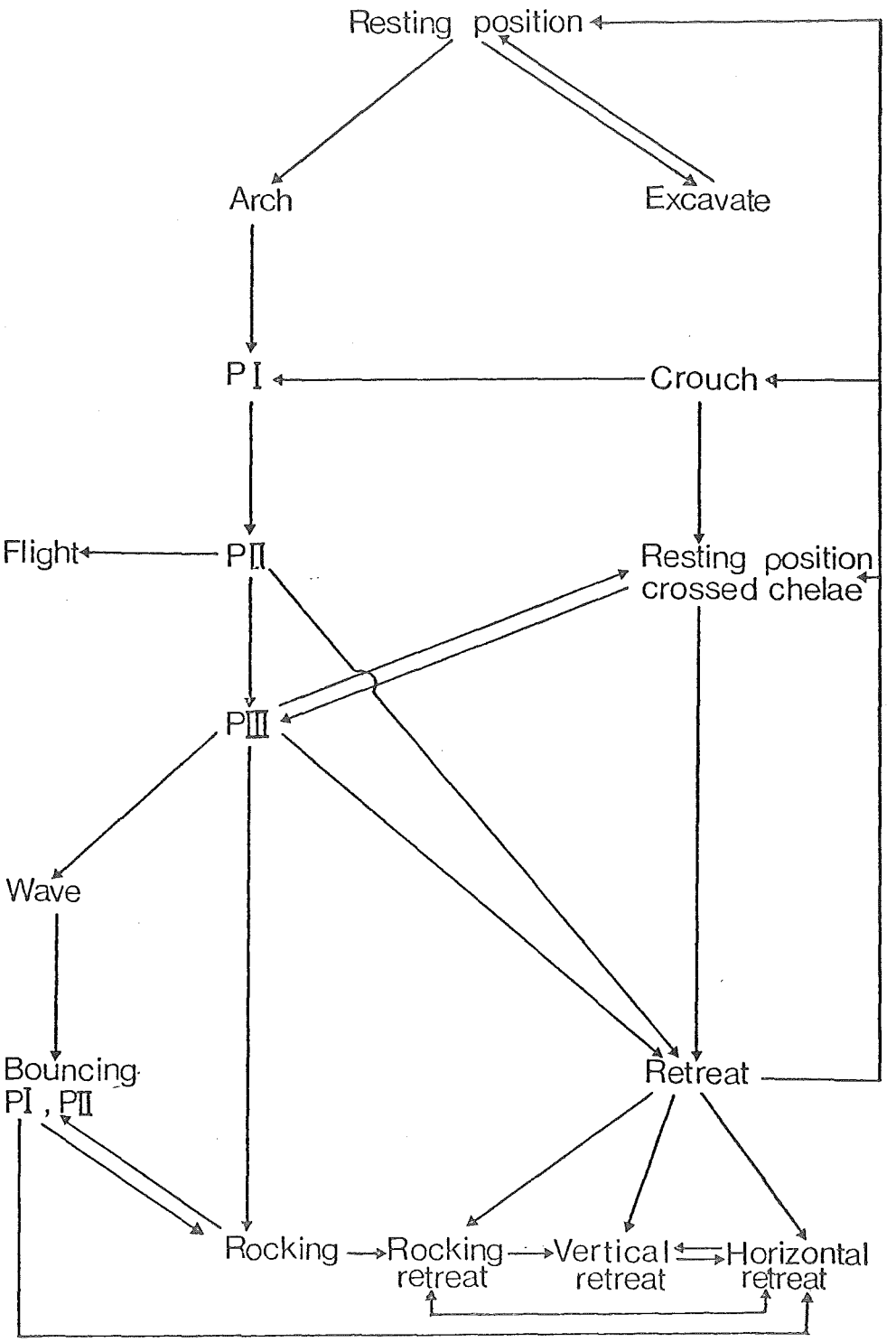


Fig. 8.15 Flow diagram of possible behaviours elicited by stimulating the side of an adult male *Notomithrax ursus* with a glass rod.

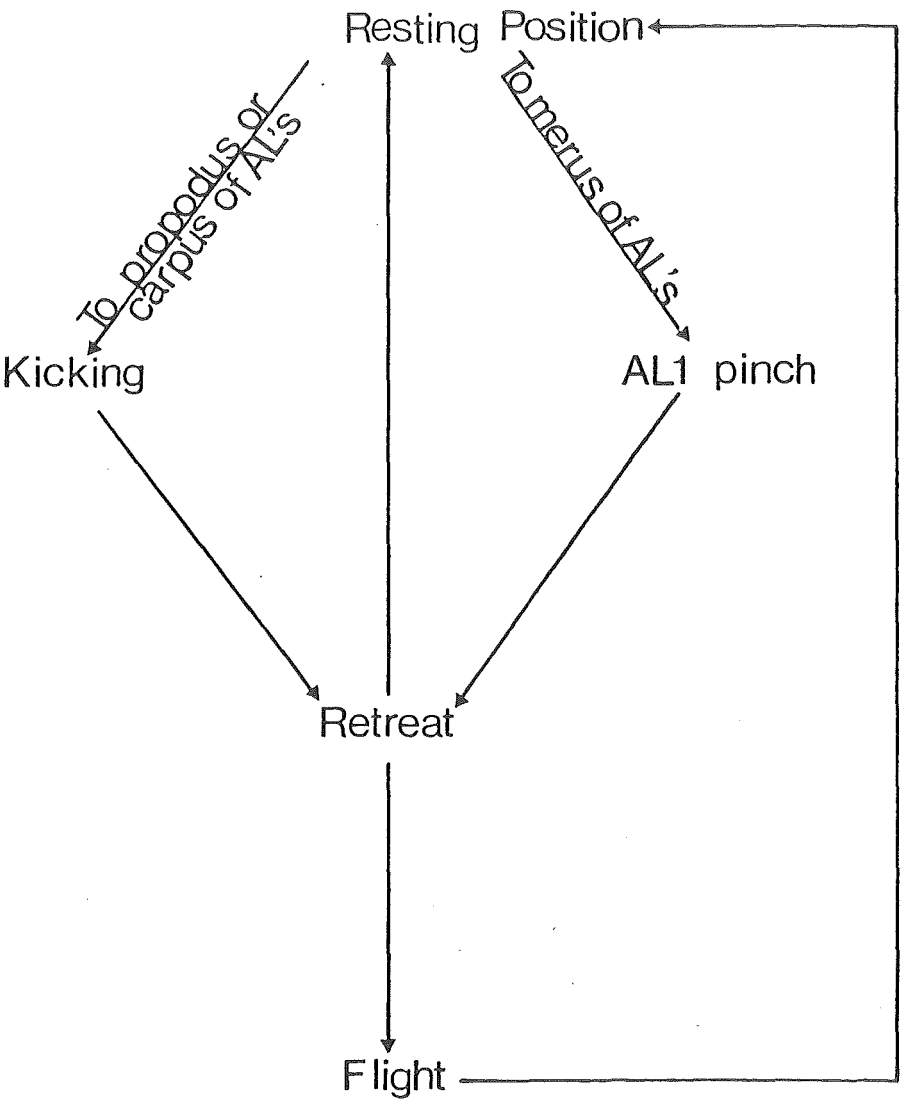


Fig. 8.16 Flow diagram of possible behaviours elicited by stimulating the side of an adult male *Notomithrax ursus* with a glass rod.

away from the stimulus. During a 'bound' the crab raised the leading portion of the body and AL's 1 - 3 and pivoting on and then pushing against the substrate with the AL4's propelled itself up into the water in an arc coming to rest one to two crab lengths in front of its launching position.

Rear stimulation elicited the same defence behaviours as elicited by a conspecific adult male. However, retreat took one of three forms: normal horizontal, rocking (both of which have been described previously) and vertical retreat.

Vertical retreat

If stimulated while against a vertical surface, such as a rock face or glass aquarium wall, *N. ursus* pressed its body flat against the surface and moved vertically sideways away from the stimulus making no attempt to orient itself on to the ground. Vertical retreat was also exhibited if the crab was retreating horizontally and came against a vertical surface. Rather than moving along the ground by the wall the crab would move up the wall in the direction it had been travelling (i.e., rostral or caudal end first) and move along the vertical surface on the lower pair of AL's.

Bouncing was frequently exhibited in between bouts of M-S and seemed to be an ambivalent behaviour as it involved the 'arch' of fighting behaviour and the 'crouch' of flight and submissive behaviours.

Lateral stimulation elicited kicking and AL1 pinch behaviours and finally retreat.

Adult females and juveniles fled from frontal, rear and lateral stimulation by a glass rod. If cornered they would arch, display and/or give a chela pinch under *extreme* provocation. Although their form did not differ from that seen in males, by comparison these behaviours were very difficult to elicit in females and juvenile males.

Cotton swab across the dorsum. Increasing the area of contact by fixing a cotton swab to the end of the glass rod and passing this across the dorsum elicited freeze behaviour if the crabs were buried. If the crabs were on the substrate within one to two crab lengths from

algae or overhanging objects they hid especially if approached from the side or back. Frontal or rear stimulation to an exposed crab elicited freezing or flight, and if the stimulation was excessive, excavating behaviours. Lateral stimulation to an exposed crab elicited freeze or retreat behaviour.

The addition of the cotton swab resulted in the crabs reacting to the rod approaching frontally from as far away as 5 cm.

(c) Chemotactile stimuli

(i) Octopus swab. A cotton swab which had been rubbed along the suckers of an octopus elicited flight and, if possible, hiding from exposed crabs, while buried crabs froze. Flight was extremely rapid and freezing was maintained generally for periods of 3 - 4 min (maximum 10 min) after a single contact with the swab.

(ii) Small, freshly killed octopus. Brushing the dorsal surface of *N. ursus* with a freshly killed octopus elicited the same reactions as the octopus swab.

(iii) Live octopus. When contacted by a free-ranging *Octopus maorum*, or merely a tentacle through plastic mesh, *N. ursus* froze. Flight behaviour was not observed. When the crab was unbalanced by the tentacle wrapping round them *N. ursus* inevitably flexed, adducting all the appendages in to the telson. When dropped these flexed crabs lay completely motionless in the position in which they landed for up to ten minutes. Flexion is described in detail below.

(iv) Human hand. As difficulties were experienced in controlling the behaviour of the octopus to produce the appropriate stimuli, the reactions of *N. ursus* to unbalancing and general handling by a 'predator' were studied by using a human hand as a stimulus. Handling of the crabs also revealed some additional behaviours.

Seizing the AL's. Seizing one or several ambulatory legs by their propodi or carpi elicited the AL kick reaction.

Autotomy

In juvenile *N. ursus*, if an AL was caught fast or the crab was

lifted off the substrate by an AL the trapped leg was autotomised. Similarly, juveniles occasionally autotomised a cheliped.

Seizing the carapace margin. When grasped by the carapace margin, *N. ursus* repeatedly gave the AL1 arch which effectively pinched one's fingers against the anterolateral spines with painful results for the 'attacker'. When the crab was grasped by the carapace margin and lifted off the substrate the limbs were reflexively extended.

Limb extension

The ambulatory legs extended straight out from the body in a tonic contraction and the chelipeds were spread fully and, likewise, held stiffly. In this state, the limbs resisted being bent and the crabs were consequently extremely difficult to hold as they were effectively too large to enclose in the hand. This tetanus lasted for several minutes.

(d) Unbalancing *N. ursus*

Unbalancing *N. ursus*, particularly inverting it on its dorsum, elicited a reflexive flexion behaviour whether the crab was inverted by octopus, human hand, or mechanical stimulus and regardless of whether the crab was in or out of water.

Flexion

(1) Ventral aspect (see Plate 8.1)

The motionless crab rested on the sculptured dorsum. The antennal flagella were held parallel to the longitudinal axis of the body, by flexion of the basal antennal article - first segment, and the third segment - flagellum junction, and lay over the motionless mouthfield. The antennules were also motionless and adducted. The eyes were retracted against the post-orbital spine so that they did not project from the carapace margin. The red, white and blue chelipeds were tightly adducted in the inverted 'V' position so that their M-C joints met over the third maxillipeds. The chela tips were closed and rested on the thoracic-coxal joint. All AL's were adducted across the ventrum, by bending of their M-C joints, and held so that the carpus, propodus and dactyl of each were held tightly against the thoracic sternum. The left AL1 lay slightly

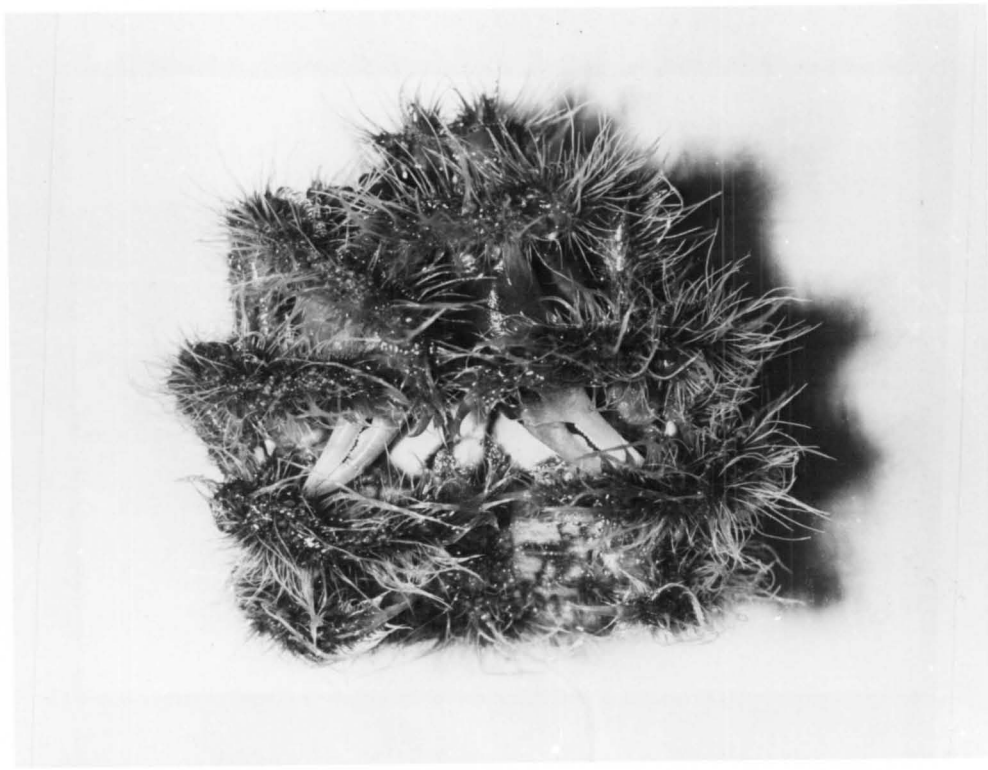


Plate 8.1 Ventral aspect of an unmasked adult male *Notomithrax ursus* in the flexed position.

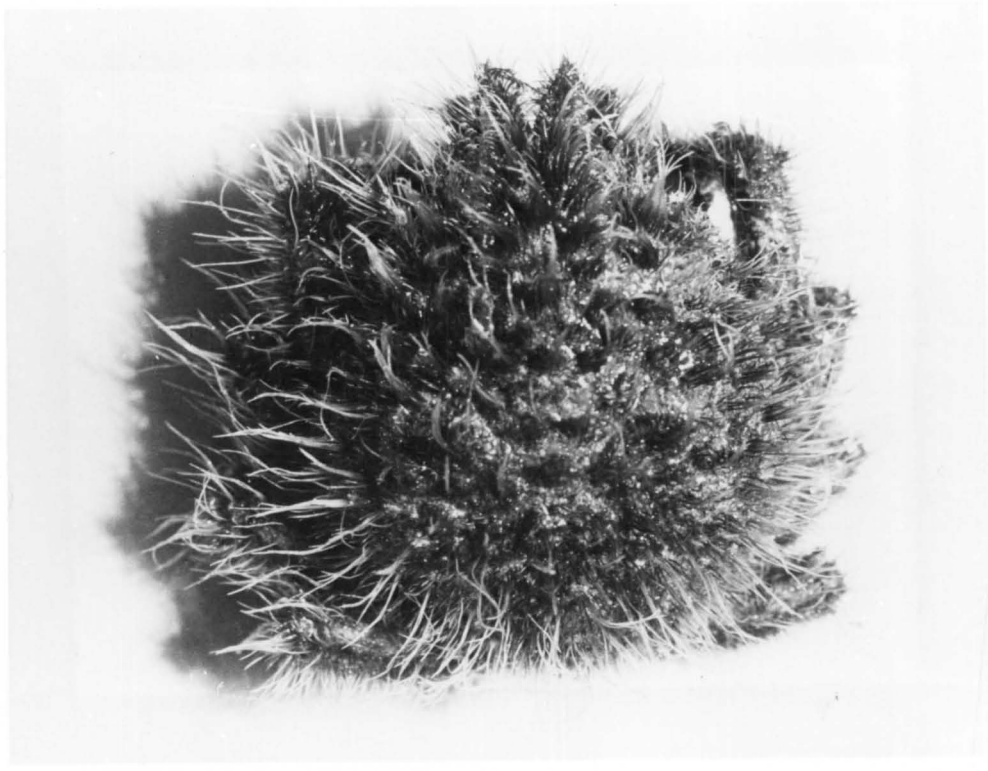


Plate 8.2 Dorsal aspect of an unmasked adult male *Notomithrax ursus* in the flexed position.

over the right AL1 and all other AL pairs lay opposite each other. In this adducted position the legs covered and effectively concealed the contrasting colouration of the thoracic sternum, the third to sixth pleon segment and all bar the carpus of each cheliped. When viewed postero-ventrally, only the first and second pleon segments were visible, while only the double ridged red carpi were visible from the antero-ventral aspect.

(2) Dorsal aspect (see Plate 8.2)

The whole body was flattened against the substrate such that the antennae, third maxillipeds, antennules and eyes were not visible when viewed from any angle. The carpus of each cheliped was visible, but only from the antero-dorsal aspect, while the merus of each AL was visible from any aspect. Viewed dorsally, the flexion posture was identical with the 'crouch' posture.

(3) Overall aspects of the flexion posture

From both the ventral and dorsal aspects, the flexion posture gave *N. ursus* an overall beehive shaped outline, the rostrum forming the apex of the 'hive'. The hair tufts softened this outline, especially around the legs and the mask served to soften the outline even further. Flexion was characterised by a complete lack of movement from the closely adducted appendages.

(4) Comparison with other postures

To determine the possible function(s) of flexion behaviour, the ventral aspect of this posture was compared with the ventral aspects of postures attained by an *N. ursus* attempting to right itself, and a dead individual (see Plate 8.3 and Table 8.2). In addition, Table 8.3 compares the dorsal aspects of the flexion, resting and crouch postures.

Righting behaviour

When inverted, *N. ursus* eventually had to turn itself over so that it was dorsal side uppermost in order to move away. 'Righting' was achieved by extending and spreading AL pairs 1 - 3 out from the body. These legs were then adducted back towards the dorsum until they made contact with the substrate. The AL4's were extended and then bent at the M-C joint until the carpus was perpendicular to the merus. The

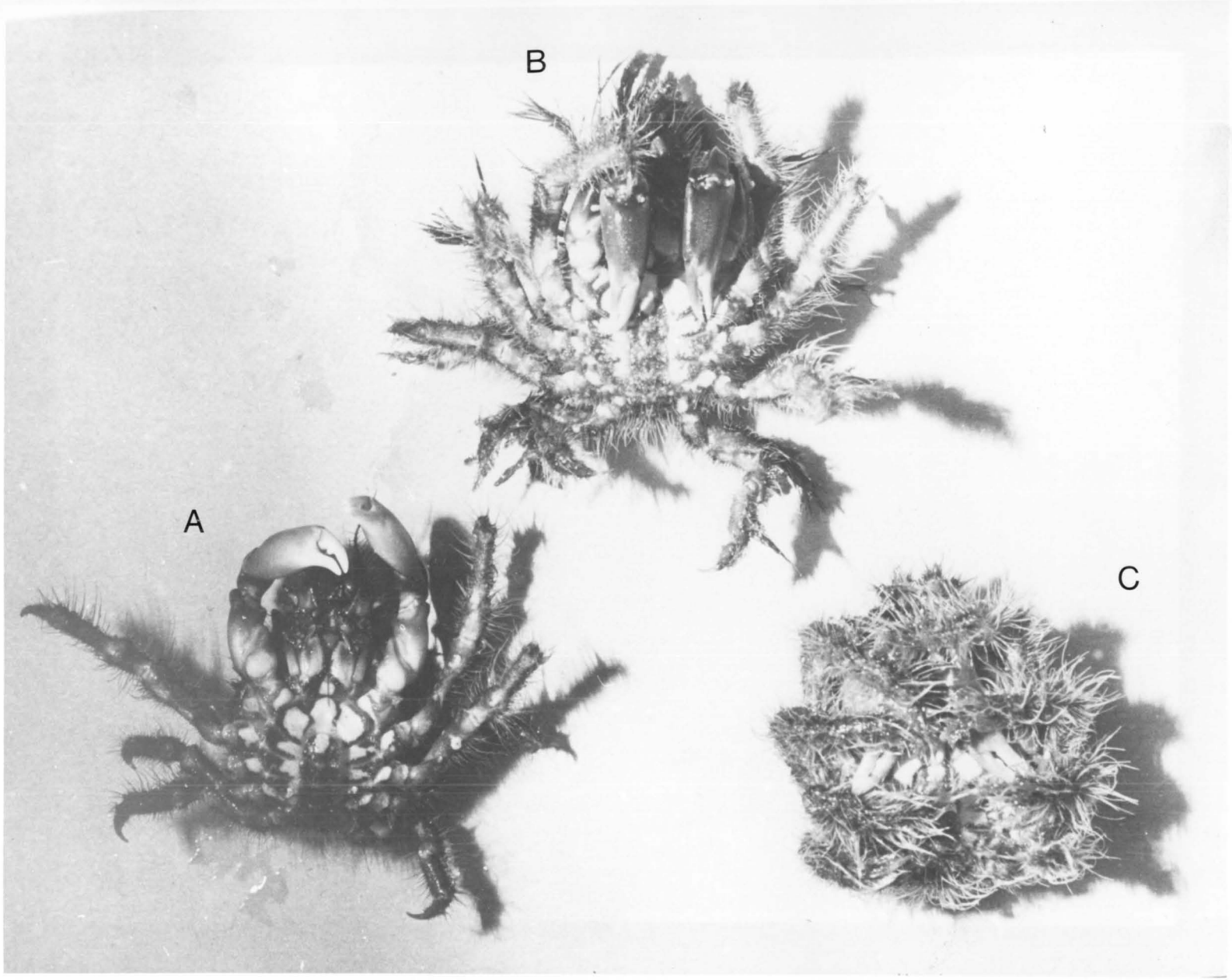


Plate 8.3 Ventral aspects of postures attained by a dead (A), and a live flexed (C) unmasked adult male *Notomithrax ursus* and one which was attempting to right itself (B).

Table 8.2 Comparison of the positions maintained by a flexed, dead and 'righting' *Notomithrax ursus*.

	Flexed	Dead	Righting
Body	Rested motionless on sculpturing	Rested motionless	Rocking on sculpturing
Antennae	Adducted and motionless	Motionless - projecting forward from rostral area	Moving - projecting forward from rostral area
Antennules	Adducted and motionless	Motionless - projecting forward from rostral area	Moving - projecting forward from rostral area
Eyes	Retracted against post-orbital spine	Projecting 45° from post-orbital spine	Projecting 45° from post-orbital spine
3rd maxillipeds	Motionless and adducted	Limp, spread apart	Moving
Chelipeds	Adducted tightly in inverted 'V'. Motionless	Spread out and lying back on substrate, any way they fell	Loosely adducted to ventrum or spread and adducted toward dorsum/ substrate
Chelae	Tips closed	Tips slightly parted	Tips slightly parted
AL's	Adducted into ventrum, motionless	Spread, as fell, motionless	Spread, arched towards dorsum/ substrate, especially AL4's, moving
Ventral colouration	Concealed	Totally exposed	Totally exposed
Cheliped	Only carpus exposed	Totally exposed	Totally exposed
Rigidity	Tonic contraction	Pliable	Moving
Motion	None apparent	None	Mouthparts, chelipeds and limbs all moving
Overall aspect	Beehive, indistinct soft outline	Oval, spiky, distinct outline	Oval, spiky, distinct outline

Table 8.3 Comparison of the dorsal aspects of the flexed, crouch and resting postures of *Notomithrax ursus*.

	Flexed	Crouch	Resting
Body	Lowered	Lowered	45° angle to substrate
Antennae	Not visible	Not visible	Visible and moving spasmodically
Eyes	Not visible	Not visible	45° angle to post-orbital spine
Chelae	Adducted inverted V	Adducted inverted V	Adducted loosely or PI
AL's	Adducted	Adducted	Extended, flexed at M-C joint
Rigidity	Tonic contraction	Rigid	Relaxed
Motion	Immobile	Immobile	Slight movements
Overall aspect	Beehive	Beehive	Oval, spiky, distinct outline

distal ends of the AL4's were then adducted towards the substrate until the dactyls could maintain a firm grip (see Plate 8.3a). The body was then levered on to the ventrum by rotation of the M-C joint. Leverage was initially assisted by the other AL's pushing against the substrate. Frequently, the AL3's were used in the same capacity as the AL4 pair, in which case leverage was occasioned first by the AL3, and then the AL4 pair.

Table 8.2 shows that lack of motion is the only attribute shared by the postures attained by flexed and dead *N. ursus*. From the ventral aspect, flexion differs from the other two postures by its overall outline, the adduction and tetanus of the appendages and the concealment of the ventral colouration. The dead crab, and the individual attempting to right itself, only differed in the extent of movement shown. At any one instant in time both postures were very similar. From a dorsal aspect, the flexion posture is identical to the crouch posture except that flexion was maintained for greater periods. Both these postures differed considerably from the normal resting posture in their overall outline, especially lack of visible movement and orientation of the body and limbs with respect to the substrate.

Flexion was elicited by unbalancing, particularly by inverting and enclosing *N. ursus* by the stimulus. The movements involved in attaining the flexed position were extremely stereotyped, but the final position attained by a crab varied depending on the strength of the stimulus. However, all crabs showed all degrees of flexion. The different intensities of flexion were revealed by the distance between the dactyls and the pleon. At the highest intensity the dactyls rested on the pleon. When in flexion, the crab was in a state of tetanus (i.e., the body and limbs were in a state of extreme muscular rigidity) and the body resisted any forcible movement of the appendages. When dropped while flexed *N. ursus* were capable of remaining as they landed, holding very unnatural positions, such as balancing on their rostral area. However, the position held depended on the strength of the eliciting stimulus. A strong stimulus, such as grasping by an octopus tentacle resulted in *N. ursus* remaining as they fell. However, if inverted by a mechanical stimulus they only remained as they were if they

landed ventral side up. If they fell on their side, front or tipped any other way so that their AL's contacted the substrate, they attempted to right themselves.

Flexion was subject to habituation, the duration the posture was held decreasing with successive exposure to the stimulus. Once habituated, flexion could be induced, in all crabs, by gently stroking the ventral surface, forcibly bending the legs back towards the dorsum or by lifting or stroking the abdomen. Lifting of the abdomen was particularly effective in females.

Analysis of photographs of the ventral aspect of *N. ursus* indicated that there were no differences in flexion behaviour attributable to sex, maturity or size of the individual, nor to the presence or absence of the mask.

Generally, when reverted to the normal orientation ('righted'), *N. ursus* did not stay in the flexed or crouch position but, if in contact with the substrate, immediately extended its legs and chelipeds to the resting or locomotory position and to the fully extended position if off the substrate. This correlation between leg position and orientation of the crab with respect to gravity indicated that flexion was controlled by the statocysts rather than stimulation to the hair tufts. Upon landing on the substrate and being dorsum uppermost the crabs either froze or moved off, rocking as they went.

8.4 DISCUSSION

8.4.1 Perception

Crabs have well developed visual, tactile and olfactory systems (Waterman, 1961). The sensory capabilities of *N. ursus* were not investigated as such, although the inference that visual, tactile and chemical cues are utilised during general maintenance, agonistic and predatory/anti-predatory behaviours can be drawn from the responses elicited by various stimuli.

(a) Vision

These crabs were strongly photonegative, avoiding white light

unless directly confronted by it when they were exposed, whereupon they froze. Freezing was also elicited by sudden exposure to red light, but *N. ursus* habituated and within seconds would recommence their previous behaviour. This lack of sustained reaction to red light suggests that, like the closely related majid *Libinia emarginata* (Wald, 1968), the spectral sensitivity of *N. ursus* may also move toward the violet end of the spectrum when adapted to red light. In addition, *L. emarginata* possesses two visual pigments, differentiated not for colour vision but for use in dim and bright light as are vertebrate rods and cones. The possession of a similar dual pigment system by *N. ursus* would explain why these nocturnal crabs were so very sensitive to visual cues even under dim red light.

Schone (1968) maintained that the agonistic activities of aquatic forms seemed to depend mainly on tactile and possibly chemical stimuli, while in semi-terrestrial species agonistic behaviour was predominantly based on visual information. However, that vision played an important part in the agonistic behaviour of *N. ursus* is supported by the following:

(1) *N. ursus* displayed at a distance of two to three crab lengths from one another during both dim red light and starlight;
(2) an adult male displayed to its own image for over five minutes;
(3) the meral-spread display revealed contrasting markings on the ventrum and chelipeds;
(4) meral-spread displays have been recognised in all brachyurans which have visual displays (Schone, 1968).

Vision has also been found to be important in a wide variety of aquatic Crustacea (Bovbjerg, 1956, 1960b; Teytaud, 1971; Swartz, 1976; Sinclair, 1977). Hazlett found that in the hermit crab *Clibanarius vittatus* (1972a) and the spider crab *Microphrys bicornutus* (1972b) the final cheliped posture was more important than the movement to the final posture. Consequently, the evidence indicates that vision is more important than was generally thought for aquatic Brachyura.

Aggressive displays exposed the ventral red, blue-grey and white markings suggesting that colour was an important cue. Although there is strong evidence to support that some Crustacea possess dichromatic vision (Goldsmith & Fernandez, 1968; Wald, 1968; Autrum & Thomas, 1973) the only majid crab studied to date, *L. emarginata*, lacks the ability to perceive

colour (Wald, 1968; Hays & Goldsmith, 1969; Wolken, 1971). In addition, *Libinia* (Pearse, 1911), *Maja, Pisa, Inachus* and *Stenorhynchus* show no evidence of being able to discriminate colours in behavioural experiments. Consequently, it seems unlikely that *N. ursus* respond to the difference in hue of the ventral markings of conspecifics. However, *L. emarginata* has two visual pigments differentiated, not for colour vision, but for use in dim and bright light (Wolken, 1971) and they are known to be selectively sensitive to polarised light (Eguchi & Waterman, 1966). *N. ursus* may respond to the intensity differences of the ventral markings. Hazlett (1972c) hypothesised that *Calcinus tibicen* may respond to the contrast in brightness and not to the particular hues of the colour pattern. That contrast may be important was reinforced by the fact that *N. ursus* was extremely sensitive to both lateral and overhead shadows larger than themselves, under both red and white light. This sensitivity to shadows is shared with another majid *Pisa tetraodon* (Milligan, 1915).

Finally, *N. ursus* were also sensitive to the movement of stimuli outside the aquaria, so motion must be perceived at least partly by the visual sense. It is interesting to note that Horridge & Shepherd (1966) found that crab eyes assessed real motion by following the centres instead of the edges of large areas. This type of movement assessment could have unfortunate results with a predatory octopus as it is the edges (tentacles) and not the centre (body) which generally does the attacking.

(b) Chemotactile perception

Knudsen (1964b) maintained that the visual and tactile senses of the spider crab *Pugettia producta* were the most highly developed for feeding and that the chemical sense was not very extensively used. However, the gathering of food and algae, as well as the general exploration of the surroundings by *N. ursus*, appeared to be mediated through the olfactory and tactile senses not through vision. Food, placed out of reach but directly in front of the eyes, was located by cheliped exploration, not by a directed grasp of the chela as one would expect if vision was involved. Yet *N. ursus* oriented the chelae directly to any food or algae which brushed against the AL's or chelipeds. These results are in agreement with Field (1977) who stated that, "Chemical stimuli predominate in eliciting feeding behaviour of marine crustaceans", and Barber (1961) who concluded that the antennae, antennules, mouthparts, chelipeds and walking legs were all very sensitive to chemical stimuli. The majids *Inachus*

dorsettensis and *Stenorhynchus* are reported to find their food almost exclusively by scent (Pearse, 1911). Neurophysiological and behavioural studies have shown that in various Crustacea, including the spider crabs *Pugettia* and *Libinia*, feeding and walking responses are initiated by extreme low concentrations (5×10^{-4}M - 10^{-12}M) of amino acids and related amino compounds (Case & Gwilliam, 1963; Fuzessery & Childress, 1975).

N. ursus was extremely sensitive to stimuli created by fish, human hands, gumboot clad human feet, glass rods and tapping and knocking of the aquaria walls as far away as 50 cm (i.e., 17 crab lengths). As the fish and human hands were the only stimuli which would exude animal chemical cues, water disturbance was probably perceived purely by the tactile sense.

There are only two morphological types of mechano-receptors in Crustacea, the hair receptor and the sensory neuron with its distal terminal embedded either in muscle or in connective tissue membrane (Cohen & Dijkgraafs, 1961). It is theoretically possible that the addition of algal pieces increases the sensitivity of the hair tufts so that *N. ursus* can detect potential predators via their attendant water disturbance from further afield. *N. ursus* was very sensitive to stimulation of the actual hair tufts. However, there was no difference in response given to stimulating the distal end of the algae of masked crabs and stimulating just above the hair tufts of unmasked crabs indicating that the mask does not aid the detection of distal stimuli.

(c) Individual recognition

Although it was often difficult to determine which sensory modalities were being used, their different behavioural repertoires showed that *N. ursus* could differentiate between conspecifics and predator-like stimuli. Avoidance occurred at five to six body lengths of one another indicating that *N. ursus* is capable of perceiving conspecifics at this distance. In addition, avoidance was frequently elicited by the mere presence of a larger or more 'dominant' individual among males and by the presence of any conspecific among females and juvenile males, implying that *N. ursus* can also recognise and respond to different classes of conspecifics. There was no evidence that *N. ursus* were capable of individual recognition but, as pointed out by Hazlett (1966), 'individual recognition' among arthropods may be a less

narrowly defined class as opposed to 'one particular specimen' as in humans. Since *N. ursus* had the same repertoire regardless of whether they or their opponent were masked, the algal mask did not affect their perception of each other.

8.4.2 Agonistic Behaviour

The behaviours comprising the agonistic repertoire of *N. ursus* had features which Wright (1968) held were common to all displays exhibited by crabs. Retaliation, immobilisation and flight were universal and submission was characterised by lowering the body, adducting the chelae and exposing the dorsum to the opponent. During aggression the body was raised high above the substrate, rotated back so the anterior portion of the carapace was higher than the posterior portion and the chelae were spread. Meral-spread consisted of rapid (less than 1 sec) fronto-lateral movements of one or both chelae, and was the same behaviour as that reported for the other aquatic brachyuran families (Schone, 1968). Wright's (1968) three intensities of high, medium and low meral-spread were clearly recognisable.

Between males an encounter often led to physical interactions such as striking or grasping with the chelae which, in turn, terminated in wild fights. When compared with semi-terrestrial forms such as grapsids and ocypodids, the agonistic encounter did not appear to be highly formalised. I observed a relatively wide variation both in the sequence of action patterns during an agonistic encounter and in the orientation of the display with respect to the partner. Wright (1968) and others have cautioned that such variation may be a laboratory artefact and this would need to be checked by further field studies of the agonistic behaviour of *N. ursus*.

The threat postures and formalised and wild fights of *N. ursus* were the same as those described for the spider crabs *Maja squinado*, *M. verrucosa*, *Eurynome aspera* and *Stenorhynchus seticornis* (Schone, 1968). However, the AL parallel behaviour was not as common as that reported in the spider crab *Microphrys bicornutus*; nor was it elicited by the lateral approach of a stimulus (Hazlett, 1972b).

N. ursus exhibited several behaviours which have not been reported previously for the Majidae. Waving of the chelae has only been reported for the Ocypodidae (Crane, 1941) and is in a totally different plane than that seen in *N. ursus*. Tapping and envelopment have been reported in the Xanthidae by Sinclair (1977). Grasping has been reported in the Xanthidae (Sinclair, 1977) and in *Petrolisthes* spp. (Molenock, 1976), however, grasping of the hair tufts seems to be unique to *N. ursus*. Pushing has been reported in many families (Schone, 1961; Vannini & Sardini, 1971; Molenock, 1976). The mutual chela strike of *N. ursus* has several elements in common with the meral slap of the Xanthidae (Hazlett, 1975b) and may, in fact, be a part of ritualised fighting. Ritualised fights often ended when one of the participants attempted to tip its adversary over, whereupon a wild fight ensued. Tipping has been reported in *Calcinus laevimanus* (Anomura) (Reese, 1962), *Orconectes virilis* (Astacura) (Bovbjerg, 1953), and the river crab *Potamon fluviatile* (Herbst) (Vannini & Sardini, 1971). In *C. laevimanus* this behaviour became ritualised and assumed the significance of a submissive posture as the subordinate hermit crab spontaneously turned itself over when neared by the dominant animal. In *P. fluviatile*, once the opponent was tipped over, the aggressor immediately abandoned its hold and remained immobile while the loser righted itself and fled. Although *N. ursus* were never observed to completely tip an opponent over, it is feasible that when they are successful the loser flexes as it does when unbalanced by predator-like stimuli. In which case, the immobility of flexion may inhibit further aggression from the victor.

The agonistic behaviour of *N. ursus* was more complicated than that usually reported for totally aquatic brachyurans (Schone, 1961; Wright, 1968; Teytaud, 1971; Hazlett, 1972a, b, 1975c; Sinclair, 1977). The classification of the behaviour of *N. ursus* was as natural as possible. However, because of the difficulties of studying nocturnal, fully aquatic animals, it is possible that the complexity of behaviour observed was, in fact, caused by misinterpretation. However, I was able to gather information on agonistic behaviour from innumerable situations and stimulus variations (e.g., from the diurnal study and from the predation experiments in Section II). The majority of other studies have been conducted under comparatively restricted circumstances. In addition, Vannini & Sardini (1971) found that the aquatic river crab *Potamon fluviatile* also had a very extensive repertoire of agonistic behaviours. Hence I agree with

Swartz (1976) who, from a study of the xanthid *Neopanope sayi*, believed that the attempt to construct a dichotomy between the behaviour of aquatic and semi-terrestrial brachyurans may not be valid.

The laboratory conditions controlled all the variables known to affect agonistic behaviour except which crab initiated the interaction (Rubenstein & Hazlett, 1974; Molenock, 1976) and the distance between participants (Jackowski, 1974). Both of these uncontrolled variables exerted a considerable influence on the agonistic behaviour exhibited by *Notomithrax ursus*. Under the natural and semi-natural conditions in the laboratory, the majority of potential interactions never eventuated because, during their active phase, all classes of *N. ursus* avoided one another when they came within five to six body lengths of one another. In contrast, there was a high incidence of interactions between *N. ursus* under the confined conditions in the observation aquarium as they were unable to hide or escape completely from one another.

Females and juvenile males continued to attempt to avoid all conspecifics but especially the adult males, who displayed to all crabs but only engaged in actual combat with other adult males. Smaller adult males avoided larger adult males and moulted crabs, regardless of class, avoided all conspecifics. This 'dominance' of male over female and juvenile, and large over small adult males, had been recorded in other Crustacea (Crane, 1941, 1958; Douglis, 1946a, b; Bovbjerg, 1953, 1956, 1960b; Lowe, 1956; Beer, 1959; Reese, 1964; Cameron, 1966; Warner, 1970; Vannini & Sardini, 1971; Sinclair, 1977). Among the females and juvenile males 'dominance' was settled by shoving or pinching the adversary. Retaliation behaviours were non-existent among these classes.

'Subordinate' *N. ursus* always attempted to retreat without fighting and generally adopted the low crouching position. 'Subordinate' behaviours were observed to follow active fighting between adult males, a threatening posture or chela strike by an adult male to females and juvenile males, or to a small adult male, and a chela shove or push by a higher ranked animal.

In the introduction it was postulated that the algal mask may have been an assessment cue of fighting ability which was used in agonistic and/or courtship behaviour. However, although only adult males displayed and engaged in escalated fights, there were no sex or maturity differences

in algal masking behaviour (i.e., masking incurred the same cost to all *N. ursus*). Consequently, it is highly improbable that the mask is an assessment cue of fighting ability.

In the laboratory, at least, wild fights were more prevalent than ritualised fights, a phenomenon which has been reported in other majids (Schone, 1968; Wright, 1968). In addition, the escalation of an encounter to a fight was more common than display indicating that the postulate that the mask impaired the assessment of size may be correct. However, the behaviour of *N. ursus* remained unchanged regardless of the presence/absence of the algal mask on themselves or the other participant(s) in an encounter. Consequently, the mask cannot be considered to affect the assessment of size, nor any other distinguishing character of individual *N. ursus*. In addition, it cannot effect an increase in the contrast provided by the cheliped and ventral markings either. Hence, escalation was more likely to be a function of the stressful conditions of the observation tank, in particular the lack of space. Although no deaths occurred during laboratory observation periods, the high incidence of cheliped loss among the adult males, kept in the holding aquaria, suggested that fights may well be injurious to the participants.

In summary then, although the mask did not have any demonstrable signalling function, the intraspecific agonistic behaviour of *N. ursus* effectively dispersed these crabs.

8.4.3 Behaviours Conducive to Crypsis

Spacing out is advantageous for crypsis to be an effective anti-predator ploy. Although the presence/absence of an algal mask had no effect on the responses of *N. ursus* to 'predator-like' stimuli, the mask may very well affect a predator's perceptions of *N. ursus*. Previous chapters demonstrated that both the mask and the crab itself blend with the background and that the mask obliterates the crab's outline. In addition, *N. ursus* were active at night, rarely out from cover, and they preferred a matching background. An investigation of the individual and anti-predator behaviour of *N. ursus* showed that *N. ursus* exhibited several further behaviours believed advantageous for maintaining crypsis.

(a) Individual behaviours

As well as selecting the appropriate background, a cryptic animal should also adopt a characteristic resting attitude and the investigation of the individual behaviours of *N. ursus* showed this to be the case. In the resting position the limbs were adducted, affording *N. ursus* a smoother ball-like outline. In addition, the bright ventral and cheliped markings were concealed by the longer algal pieces which were oriented on the rostral area to hang forward over the slightly raised anterior region (Plate 1.2) making this area inconspicuous when viewed from above. The downward orientation of the anterior of the crab when on a vertical surface also allowed the rostral algae to conceal the anterior region. When stationary during bouts of locomotion, the oral region was even less conspicuous as the body was held parallel to the substrate, although the legs may have been slightly more conspicuous compared to the resting position.

Locomotion was generally very slow with the animal creeping close to the substrate and to the human eye they resembled the detrital weed drifting slowly along. Their ability to climb from one frond to another enhanced crypsis as the crab harmonised more with the algal clumps than with the rock and mud substrate.

During withdrawal behaviours, whether vertical or horizontal, the animals were pressed close to the substrate and crept along or, if attacked, rocked backwards/forwards, again resembling wafting weed. Compared to other crabs, locomotion during flight was comparatively slow. Ocypodid crabs, running on three pairs of legs, can reach a maximum speed of 1.6 metres/second on sand (Lochhead, 1961). However, speeds in water are generally slower because of the effects of water resistance. *Panulirus* can reach a maximum of 30 - 60 cm/sec in water (Lochhead, 1961). Feral masked *N. ursus* only managed a maximum of 10-15 cm/sec. Either this relatively slow flight is an attempt to maintain crypsis or the mask increases the water resistance impairing movement. Although this problem was not studied there were no noticeable differences in the speeds attained by masked and unmasked crabs in flight.

(b) Anti-predatory behaviours

The anti-predatory and agonistic behavioural repertoires of *N. ursus* had many elements in common. *N. ursus* avoided, retreated from,

retaliated against, and, if cornered, displayed to predators. Although none of the females or juvenile males attempted to bite or strike with their chelae, however much they were stressed, the adult males pinched 'predators' with great force, a behavioural difference shared with the related masking crab *Pisa tetraodon* (Milligan, 1915). However, *N. ursus* generally emphasised those defences conducive to concealment. When *N. ursus* were confronted by large predator-like stimuli they fled and hid, buried themselves, and especially when contacted, remained completely immobile. This state of minimum locomotor activity in response to tactile stimulation to a large area of the body is common to many Crustacea (Pardi & Papi, 1961). In contrast, *N. ursus* crouched or retreated from tactile stimulation from conspecifics. This differential response to large and small tactile stimuli would be adaptive as predators are generally bigger than conspecifics. These differences in behaviour by *N. ursus* corroborate Huntingford's (1976) postulate that the major difference between inter and intraspecific aggression is the eliciting stimuli themselves and not any major difference in internal motivations.

The anti-predator responses of *N. ursus* depended upon whether they were buried, close to cover, or totally exposed. If near cover they hid, but when exposed or buried they froze and in both cases were very difficult to differentiate from normal algal tufts. Even under very bright light it was very difficult to differentiate buried *N. ursus* from naturally occurring clumps of algae. Even the actual act of excavating was rendered less conspicuous by the rocking motion it entailed, causing the crab to resemble weed wafting in the water current. Finally, the differential response of *N. ursus* to bright light was also conducive to concealment as when near a beam of light it is better to avoid it but when directly exposed to that beam of light, the deception is harder to maintain and movement could prove fatal.

When the primary defences (Edmunds, 1974) failed, *N. ursus* exhibited some interesting secondary behaviours. The AL1 pinch could well have a startle effect on the predator. For example, when searching through the algae and detritus of the intertidal area, an unexpected pinch to one's fingers caused momentary withdrawal from the area, allowing *N. ursus* to slip away. This pinching may affect other predators in a similar way. Even if *N. ursus* had been found initially, its new position among the weed entailed the formation of a new searching image. Theoretically, the AL pinch could have the same effect on other

hunters. This use of defensive armature has been noted by Robinson (1968) for males of the stick insect *Oncotophasma*. Autotomy, which left the predator holding only a leg or, occasionally, a chela, had much the same result as the AL pinch. There was a distinct maturity difference in autotomy. Only the young crabs autotomised limbs, presumably because they possess the power of regeneration which mature crabs lack. However, algal pieces of the mask of *N. ursus* can be 'autotomised' so that when the mask is grabbed the crab can run in the opposite direction. Limb extension seemed to be a mechanical defence greatly increasing the size of the animal making it very difficult to handle (or swallow).

Flexion was a particularly interesting behaviour. The appendages were all adducted into the body and held there in a cataleptic state (Bullock & Horridge, 1965) resisting all efforts at moving them. Although the appendages were adducted in a very stereotyped order, flexion did exhibit variations in intensity as shown by variations in the distance between the adducted appendages and the body.

Although both flexion and freezing occurred in response to predator-like stimuli, and both involved catalepsy of the appendages, flexion was quite distinct from freezing. Freezing occurred when the animal was the right way up and the appendages went rigid exactly as they were. Flexion only occurred when the crab was unbalanced and the limbs adducted before becoming cataleptic.

The behaviour of drawing all the appendages into the body and/or rolling into a ball is not uncommon. It occurs in woodlice and has been reported for *Ranatra* (Holmes, 1906), phasmids, e.g. *Carausius morosus* (Godden, 1972, 1974; Godden & Goldsmith, 1972), the mantids *Tenodera superstitiosa, Polyspilota aeruginosa* and *Phyllocrania paradoxia* (Edmunds, 1972), geometrid caterpillars (Bullock & Horridge, 1965), the fleas *Ceratophyllus gallinae, C. garei* and *Ctenophthalmus nobilis* (Humphries, 1971), the spiders *Epeira producta, Amaurobis candidus, Celoenia excavata* (Robertson, 1904), boids, e.g. *Candoia aspera* (Bustard, 1969), the African ground squirrel *Xerus erythropus* (Ewer, 1966) as well as several crabs, e.g. *Carcinus maenas* (Jensen, 1972).

The behaviour of drawing in the appendages and remaining rigidly motionless has variously been termed 'Eierschultzreflex' (Bethe, 1897;

Broekhuysen, 1936), sham-death (Robertson, 1904), death-feigning (Holmes, 1906), balling (Bustard, 1969), and thanatosis (Godden, 1972, 1974; Edmunds, 1974). It has also been referred to as catalepsy (von Steiniger, 1933) but as Godden (1974) pointed out, catalepsy only signifies "... the peculiar peripheral effects associated with thanatosis ...". The comparison of flexed and dead *N. ursus* showed that, visually at least, the resultant postures were markedly different. The limbs of dead *N. ursus* were limp and attained a variety of positions, and were never cataleptic. In addition, in death the ventral markings and chelae were quite apparent. Consequently, to describe flexion in *N. ursus* as death-feigning or thanatosis would appear to be incorrect. A consideration of the descriptions of the positions attained by the previously mentioned species also indicates that they do not 'death-feign' either. For example, Holmes (1906, p.213) reported that when the body of a tetanic *Ranatra* was cut in two across the prothorax, the posterior portion died after four hours and "... its original tetanic condition seemed to pass gradually into one of limpness and flaccidity ...". Holmes continued to describe a behaviour he termed 'deceptive quiet' where, when approached, *Ranatra* individuals ceased swimming, relaxed their muscles, and lay with outstretched legs. He also noted that if a dead and limp *Ranatra* was held in water its legs lay spread apart as in 'deceptive quiet', although not as symmetrically. Deceptive quiet, which is attended by a relaxation of the muscular system, is seen in the North American opossums *Didelphis* spp. (Hamilton, 1963) and the hog-nosed snake (Alcock, 1975) and appears to be true death-feigning.

Regardless of its name, the habit of adducting appendages has two major advantages in anti-predator defence (Edmunds, 1974). Firstly, it is thought to protect the vulnerable areas. Associated with this may be the inability of the predator to physically handle or consume the 'ball-shaped' prey. Secondly, the universal lack of movement which accompanies flexion/thanatosis is thought to inhibit attack from animals which require movement to elicit an attack. In addition, flexion/thanatosis may cause a predator to relax its attention, thus giving the animal a chance to escape. Flexion may also serve to confuse the predator's hunting ability. Curio (1976) reported that the snake *Coluber constrictor* detected a live cricket quicker than a dead cricket which only emitted chemical cues. However, if the live cricket 'froze' and thus ceased to offer movement as a stimulus, the snake lost contact

with it and took longer to locate it than to locate a dead cricket. It appears that sudden immobility confuses the search image. In the case of *N. ursus* flexion also served to conceal the conspicuous ventral markings, the ventral view of a flexed crab looking remarkably similar to the dorsal view of a frozen one. The resemblance is even greater when the crab was masked. As mentioned previously, flexion may also be exhibited by adult male *N. ursus* when tipped over by a conspecific adult male.

Flexion/thanatosis "constitutes a state of minimal arousal in which the animal appears oblivious to the majority of environmental stimuli" (Godden, 1974); and in *N. ursus* its main behavioural characteristic, apart from immobility, was the suppression of the normal righting reflex. The first sign of arousal was the performance of righting movements. Although flexion was maintained for variable times, arousal could always be induced immediately if the crab was turned dorsal side up again.

When turned the right way up after flexion, *N. ursus* would rock antero-posteriorly, either on the spot or as it moved away resembling algae wafting in the current. This rocking has been reported in the phasmid *Carausius morosus* as well (Godden, 1972).

In summary, not only the attributes of the mask, but also the anti-predatory behaviours and individual behaviours support the hypothesis that the mask has a procryptic function.

8.4.4 Other Postulated Functions

Dixon (1891) observed that the masking crab *Hyas araneus* sits with its chela stretched prominently forward and rocked, rotating on the AL4's. Gobies were attracted to the red and white chelae tips moving among the algae and, when the fish were within reach, *H. araneus* captured them. On the basis of this, Dixon postulated that the mask functioned both as anti-crypsis and as a contrast for the chelae 'lures'. *N. ursus* exhibited the same antero-posterior rocking as *H. araneus* but its chelae were adducted and rocking was induced by contact with a predator. In addition, *N. ursus* were never observed to actively prey upon comparatively large animals. Hence, with *N. ursus* the mask is unlikely to also function as anti-crypsis.

It has also been postulated that the mask is maintained as a supplementary food source. *N. ursus* were never observed to eat algae, but they do possess the typical serrate spoon-tipped chelae which, in the spider crab *Mithrax verrucosus* (Warner, 1977), are thought to be used for scraping algae from rocks. Certainly, *Pisa tetraodon* (Milligan, 1915), *Maja squinado* (Carlisle, 1957; Stevcic, 1971), *Pugettia producta* (Knudsen, 1964), and *Libinia emarginata* (Aldrich, 1976) have all been recorded to either eat algae or to have it in their gut. However, all these masking crabs were also reported to be omnivorous. Browsing through the algae for amphipods may well result in some algal material being accidentally ingested. This browsing behaviour, in conjunction with taking algal pieces to the mouthparts preparatory to masking, may have led to the hypothesis that masking crabs eat algae. Even if *N. ursus* and other masking crabs were restricted solely to eating algae, the utility (benefits less costs, Caryl, 1981) would be negative as these crabs live amongst algae. In addition, one would expect the amount of mask applied to be inversely correlated with the amount of environmental algae available. This is not the case with *N. ursus*, where specimens from deeper water where algae is scarce, have very little algae in their masks, and some are even completely unmasked.

In conclusion, the observations support the hypothesis that the algal mask of *N. ursus* has a cryptic, in particular a procryptic, function. In addition, observations make it seem unlikely that the mask, which harmonises with the background, functions as a visual, tactile, olfactory or contact chemical signal in intra or interspecific encounters.

SECTION I

CHAPTER 9

INTERACTION BETWEEN *NOTOMITHRAX URSUS* AND OTHER SPECIES

9.1 INTRODUCTION

Previous chapters have indicated that the mask of *Notomithrax ursus* is most likely to be an anti-predator device. In Chapter 8 it was demonstrated that the general behaviour of *N. ursus* fulfilled the criteria deemed necessary to maintain crypsis and that *N. ursus* maintained large inter-individual distances during their active period. However, *N. ursus* shares its habitat with the closely related *N. peroni* which also masks, seemingly to the same extent as *N. ursus*. The mask of *N. peroni* also blends with the background, again providing a prima facie case that the mask is cryptic. Hence, spacing out will also be of importance to *N. peroni*. Presumably, masked *N. ursus* and masked *N. peroni* appear as one 'species' to predators as they do to humans. Hence, *N. ursus* and *N. peroni* will need to space out relative to congenerics as well as to conspecifics if crypsis is to be maintained. Spacing between individuals can be achieved by limiting the density of the combined population of both species or by utilising different parts of the area or the daily or seasonal cycles. Consequently, it was necessary to determine the presence of *N. peroni* in the study area and its diurnal activity, dispersion, distribution, and life cycle relative to *N. ursus*.

To determine if the mask protects crabs from predators by rendering them cryptic, it was necessary to determine which species were capable of exerting a selective predatory pressure. Wicksten (1980) reported that -

> "the animals that prey on decorator [masking] crabs include the European lobster *Homarus gammarus*, the sea otter *Enhydra lutris* and a wide variety of fishes, octopuses, starfishes, spiny lobsters, other crabs and even sufficiently adventurous human beings."

However she provided no supporting evidence for this statement.

Baal (1953), Carlisle (1957) and Stevcic (1968, 1971) observed *Octopus vulgaris* to prey on *Maja squinado* and Hartwick & Thorarinsson (1968) observed *O. dofleini* (Wulker) to eat the masking crab *Scyra acutifrons*. *Octopus* species have also been reported to prey upon the masking crab *Mithrax forceps* (Verrill, 1908). Stevcic (1968) observed that the lobster *Homarus vulgaris* also preyed on *Maja squinado*.

The sea lion *Neophoca forsteri* is reported to be the most important predator of newly moulted *Jacquinotia edwardsii*, a non-masking New Zealand relative of *Notomithrax ursus* (Ritchie, 1970).

During a study of the natural feeding habits of the starfish *Astrostole scabra* in the field at Kaikoura, Dr J.C. Town (pers. comm.) encountered 29 instances of crabs being ingested. Twenty-one of these crabs were from six different genera, while the remaining eight were all *Notomithrax* spp. (three *N. ursus*, three *N. minor* and two unidentified spp.). While surveying paua in the Kaikoura sub-tidal area, Dr K. Sainsbury (pers. comm.) observed that the banded parrot fish *Pseudolabrus fucicola* quickly ate any *N. ursus* accidentally uncovered. In addition, the remains of *Notomithrax* spp. have been found in the gut contents of 13 species of New Zealand fish (Table 9.1). Although none of the studies were undertaken on fish from the Kaikoura region, ten of the reported fish species are common to the area, two are found occasionally and one is rare. Brough (1965) reported that a captive octopus, *Robsonella australis*, ate two 'large camouflaged' crabs.

Predators generally prey on more than one type of animal, effectively diluting their impact on any one prey species. Consequently, it was important to determine which other crabs were present and active when *N. ursus* was potentially exposed to predation.

The observations presented in Chapter 8 showed that *N. ursus* did not hunt for prey, indicating that the adaptive significance of the mask is not to conceal the cryptic crab from prey. However, the majids *Hyas araneus*, *Inachus* spp., *I. phalangium*, *Libinia emarginata*, *Maja squinado*, *Pisa tetraodon*, *Pugettia producta* and *Stenorhynchus* spp. are reported to prey upon one or more of the following animals: hydroids, bryozoans, barnacles, mussels, worms, asteroids, iechinoids, ophiuroids, and fish (Bateson, 1889; Dixon, 1891; Milligan, 1915; Carlisle, 1957; Hartnoll,

Table 9.1 Species of New Zealand fish recorded to contain *Notomithrax* (= *Paramithrax*) in their gut contents.

Common Name	Scientific Name	Reference	Area Studied	Spp. Reported
Barracouta		Graham (1938)	Otago Harbour	*Notomithrax* spp.
Bastard Red Cod	*Physiculus breviusculus*	Russell (1971)	North East N.Z.	*Notomithrax* spp.
		Graham (1938)	Otago Harbour	*Notomithrax* spp.
Red Cod	*Physiculus bacchus*	Graham (1938)	Otago Harbour	*Notomithrax* spp.
Blue Cod	*Parapercis colias*	Russell (1971)	North East N.Z.	*Notomithrax (ursus)*
		Young (1929)	Chatham Is.	*Notomithrax latreillei, N. peroni, N. barbicornis*
Rock Cod	*Lotella rhacinus*	Doake (1972)	?	*Notomithrax* spp.
Lemon Sole	*Pelotretis flavilatus*	Graham (1938)	Otago Harbour	*Notomithrax (minor)*
Maori Chief	*Notothenia angustata*	Graham (1938)	Otago Harbour	*Notomithrax* spp.
Paketi (= Spotty)	*Pseudolabrus celidotus*	Russell (1971)	North East N.Z.	*Notomithrax* spp.
Banded Parrotfish	*Pseudolabrus fucicola*	Dr K. Sainsbury (pers. comm.)	Kaikoura	*Notomithrax* spp.
Red Moki	*Cheilodactylus spectabilis*	Russell (1971)	North East N.Z.	*Notomithrax* spp.
Red Mullet	*Upeneichthys porosus*	Russell (1971)	North East N.Z.	*Notomithrax* spp.
Sand Flounder	*Rhombosolea plebeia*	Graham (1938)	Otago Harbour	*Notomithrax* spp.
Sea Perch	*Helicolenus papillosus*	Graham (1938)	Otago Harbour	*Notomithrax* spp.
Snapper	*Chrysophrys auratus*	Godfriaux (1969)	Hauraki Gulf	*Notomithrax minor*
		Godfriaux (1974)	Western Bay of Plenty	*Notomithrax minor*
		Colman (1972)	Hauraki Gulf	*Notomithrax minor*

1963; Knudsen, 1964a; Kaestner, 1967; Stevcic, 1971; Aldrich, 1976). Consequently, the failure to observe predation by *N. ursus* may have been the result of the absence of suitable prey and it was necessary to determine if there were any animals present in *N. ursus*'s habitat which could be susceptible to a cryptic crab predator.

9.2 METHODS

The methodologies used to gather information on the life cycle, diurnal activity, and dispersion of *N. peroni* were identical to those used for *N. ursus* (refer Chapters 3 and 7). However, as field observations revealed *N. peroni* to have the same diurnal activity as *N. ursus*, laboratory actographs were obtained for only four individuals (size range CL 26.8 - 28.8 mm).

The identities of the other species sharing the same habitat as *N. ursus* were determined initially by means of a complete search of the study channel the day following the December 1976 sample. Examples of every different species found along the channel were collected, preserved according to channel parts and later identified and their distribution along the channel noted. As this was an extremely time-consuming task, a total channel collection was only undertaken for December 1976. However, any unrecognised species subsequently encountered in the study channel were retained and their identity and dispersal recorded.

In an attempt to monitor the interspecific relationships (i.e., possible predators, prey and competitors of *N. ursus*) a record was kept of all animals found in close association with *N. ursus* (within one crab length). This was done from December 1976 to April 1977. As it was often impossible to count all the fast moving or high density species, the abundance of those species was recorded qualitatively. This study was concluded after the April 1977 sample as recording of the increasing numbers of *Notomithrax* present in the channel required all the available 'low tide' time.

Qualitative information on the nocturnal activity of the species present in the channel was gained during the night tide study (Chapter 7).

Information on predation was obtained by keeping records of any instances of *N. ursus* catching prey, or being attacked by predators. In addition, the different types of damage found on *N. ursus* were described and quantified.

Random gut content analysis was conducted on some freshly caught fish obtained from around the Kaikoura Peninsula. The gut contents of starfish, who evert their stomach over their prey, and octopus, who split crabs and suck out the meat, were not investigated as this would have required a sophisticated protein analysis of both the gut contents and *Notomithrax*. Qualitative gut content analyses have the disadvantage that they fail to indicate the relative importance of the items of diet or the seasonal fluctuations in the composition of the diet. However, an environmental and morphological approach to the problem, coupled with an extensive study of the gut contents of different age groups from different localities on a seasonal basis, had already been provided by the literature.

9.2.1 Fish Predation

As the gut contents only indicate what the fish would feed on (Lagler, 1949), a direct and easy method of studying the feeding and nature of food that is eaten by a fish is by aquarium observation. Laboratory experiments were conducted in the Edward Percival Field Station (EPFS) tank room with one fish species/shallow wooden tank equipped with running sea water, hiding places made from rocks, but NO algae, and exposed to natural lighting. One *Helicolenus papillosus*, one *Haplodactylus meandratus*, two *Latridopsis ciliaris*, two *Scorpoena cardinalis*, four *Pseudolabrus fucicola*, two *P. celidotus*, and one *P. miles* were used as predators. In addition, the actual interaction between the fish and *N. ursus* was observed with one individual from each of the four latter species.

9.2.2 Starfish Predation

Fifteen *Astrostole scabra*, ranging in size from 38.4 to 127 mm (from the proximal side of the madreporite to the tip of the opposite arm), were captured from Kaikoura Peninsula. These specimens were kept in a shallow aquarium in the EPFS laboratory room for three days with food and then starved for seven days. On 11 February 1978 they were then provided with eight masked (three male, five female, CL 14.4 - 20.8 mm) and eight unmasked

(four male, four female, CL 10.1 - 20.7 mm) *N. ursus*. The tank was provided with both algal covered rocks and clumps of algae. The tank was checked every day and the remaining *N. ursus* were counted and measured. The experiment was concluded after five days.

9.2.3 Octopus Predation

A small, presumably juvenile *Octopus maorum* was captured in a rock pool about 20 m from the study channel at Oaro Platform. This octopus was transported to Canterbury University and housed in a glass and concrete aquaria (see Chapter 3). The octopus was provided with a 'home' made from three rocks, but no effort was made to simulate field conditions. The tank was exposed to a 12 h light : 12 h dark regime, but it was not shielded from general laboratory disturbance. The octopus was given two days to acclimate to its new situation and then it was given live prey until it died. The prey were the crabs *Pinnotheres novaezelandiae, Petrolisthes elongatus, Hemigrapsus crenulatus, Helice crassa,* masked *N. peroni,* masked and unmasked *N. ursus* and the shrimp *Alope spinifrons*. The octopus was provided with various numbers and species combinations of prey and its responses to the prey were noted.

9.3 RESULTS

9.3.1 (a) Life Cycle of *Notomithrax peroni*

Few *N. peroni* were present in the study channel all year except for late July when there was a large influx of them (Fig. 9.1). Numbers also showed a slight peak in April when *N. ursus* were at their most abundant (Fig. 9.1). The two peaks were reflected by both sexes (Fig. 9.2) but, whereas the ratio approached unity in April (0.90 M : 1 F), in late July females greatly outnumbered males (0.33 M : 1 F) (Fig. 9.3). The fluctuations in the sex ratio shown for the remaining months was probably the result of the low numbers of individuals present in the channel (Table 9.2). The majority of the females found in late July were ovigerous (Fig. 9.4). The size distribution of the total population revealed no trends (Fig. 9.5), probably an artefact of the small sample size. This was corroborated by the fact that a wide range of sizes was only present in May and late July, both periods of relatively high abundance.

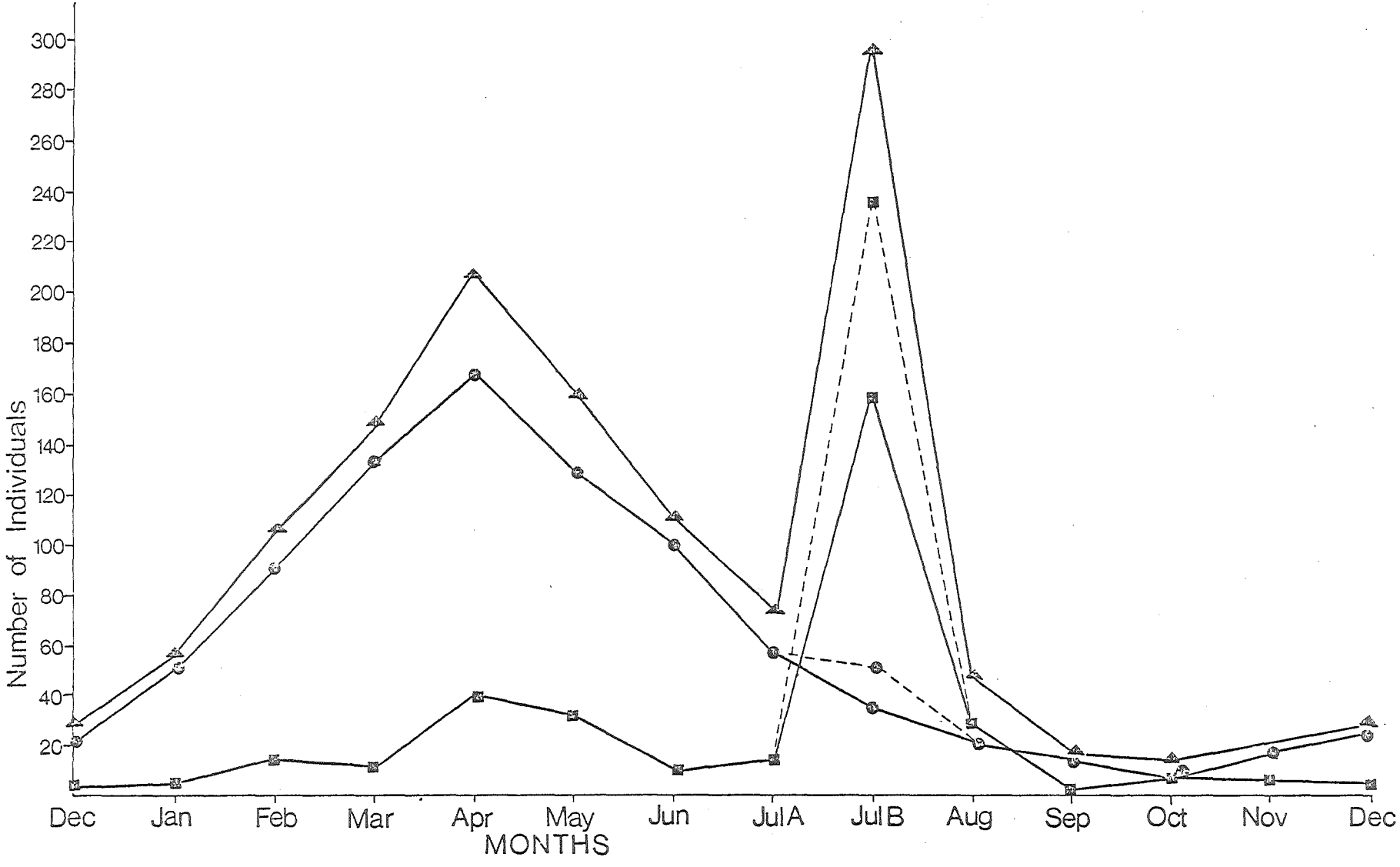


Fig. 9.1 Abundance of *Notomithrax peroni* and *N. ursus* at the study channel, Oaro Platform (1976 - 1977). Squares *N. peroni*; circles *N. ursus*; triangles, species combined. Broken line is extrapolated data (see methods, Chapter 3).

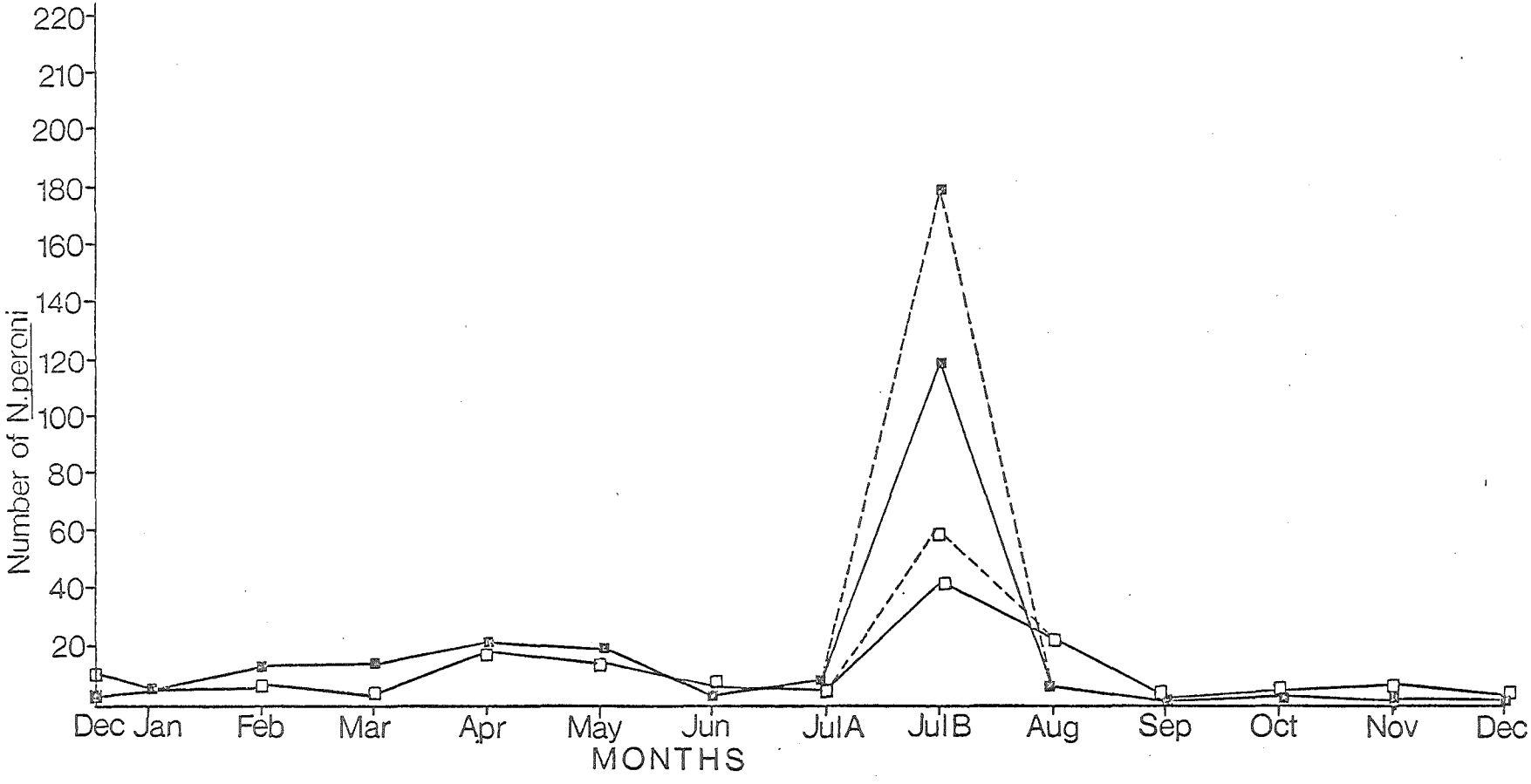


Fig. 9.2 Abundance of male and female *Notomithrax peroni* at the study channel, Oaro Platform (1976 - 1977). Open squares, males; closed squares, females.

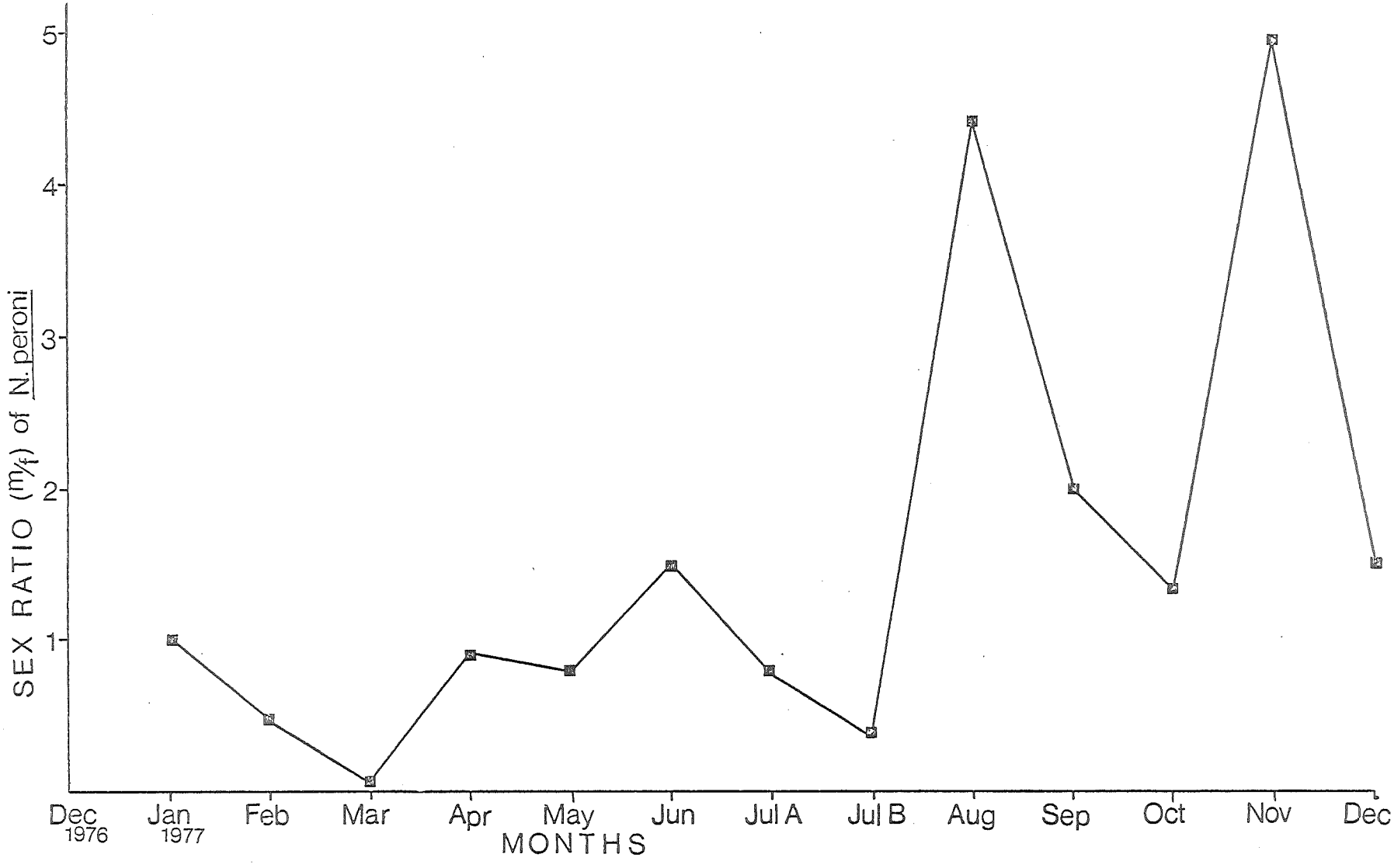


Fig. 9.3 Seasonal changes in sex ratio of *Notomithrax peroni*, Oaro Platform (1976 - 1977). Total sex ratio = 0.66. Five males, no females found in December 1976.

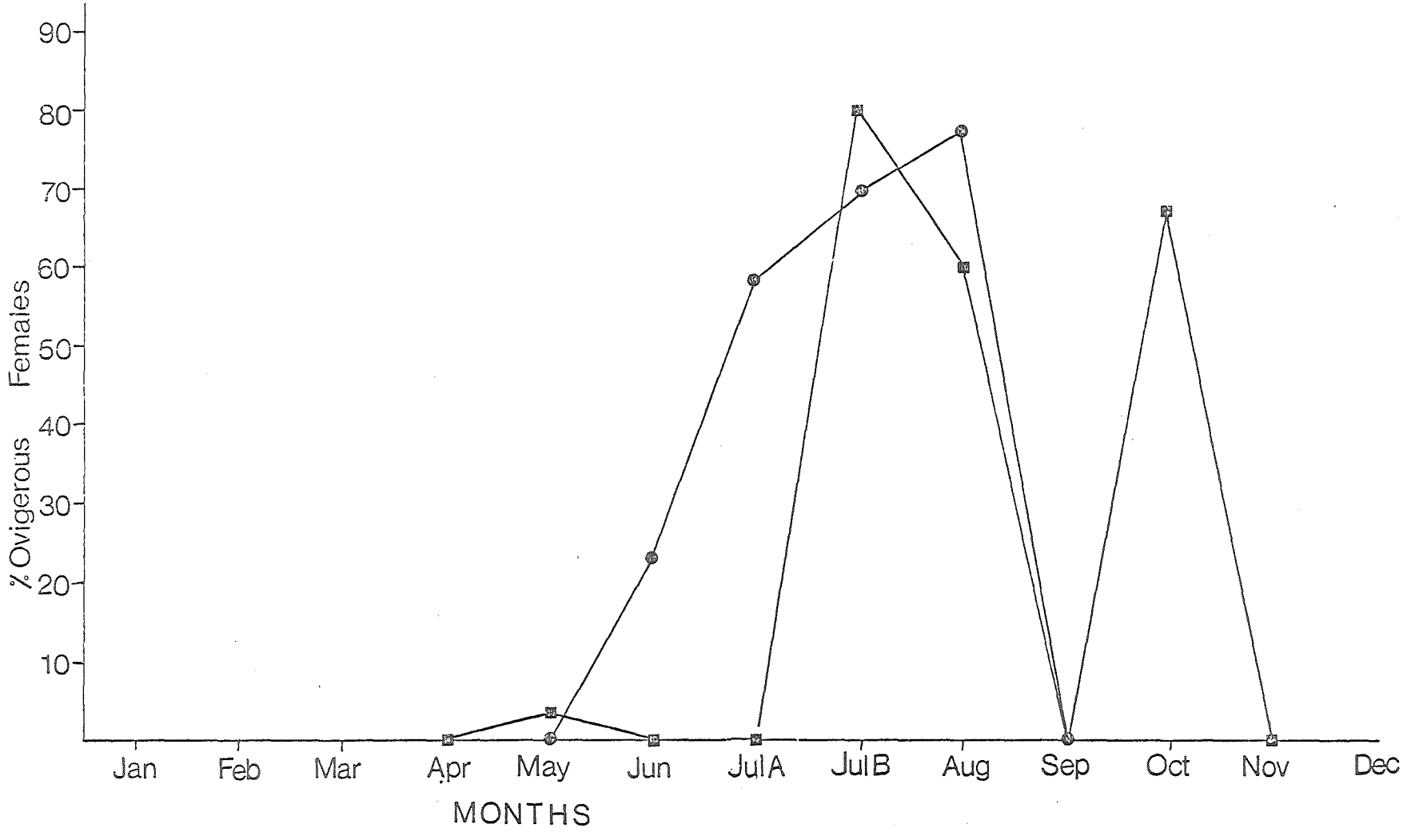


Fig. 9.4 Percentage of the female *Notomithrax peroni* sample, and *N. ursus* sample, Oaro Platform (1976 - 1977) which were ovigerous. Squares, *N. peroni*; circles, *N. ursus*.

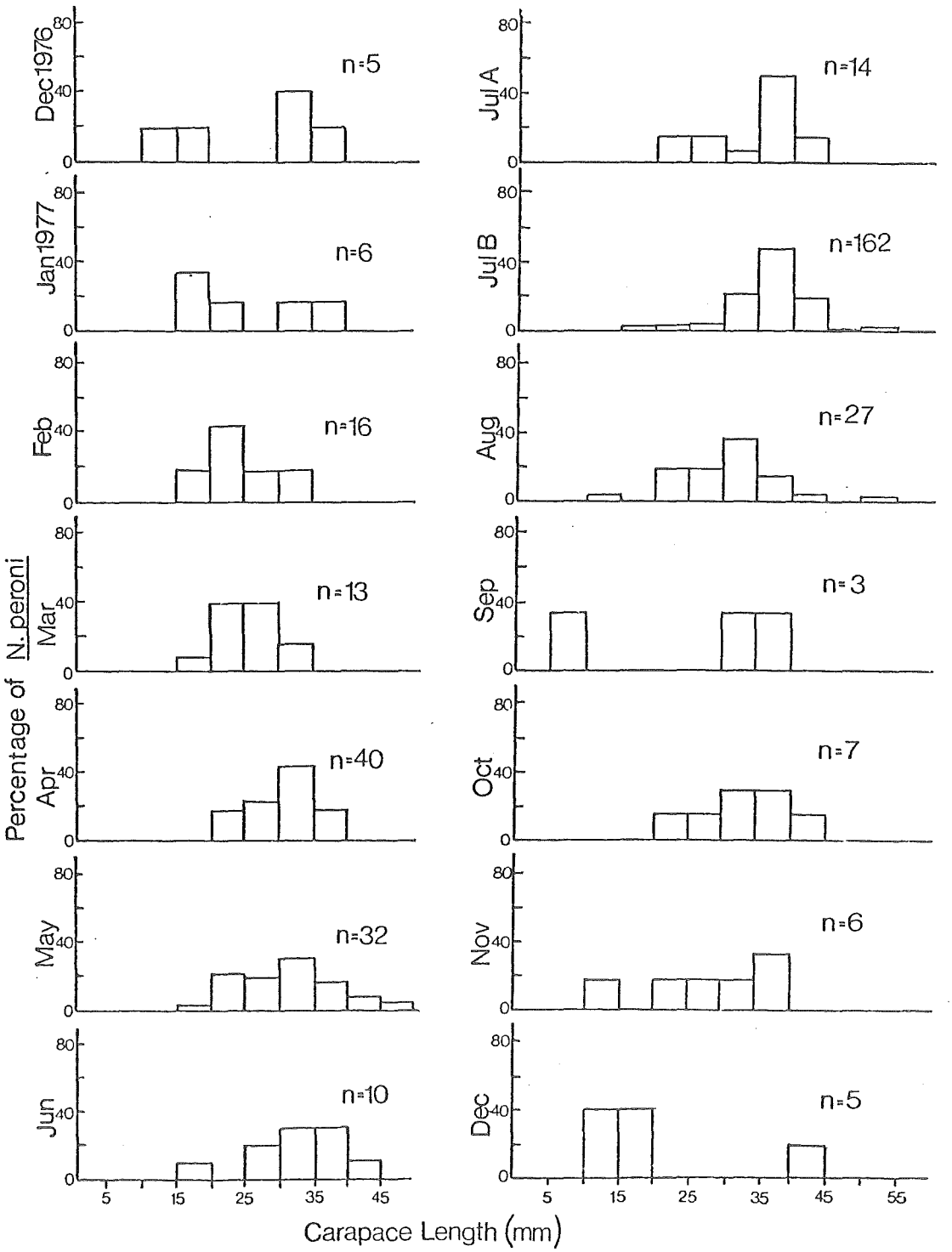


Fig. 9.5 Seasonal changes in size-frequency distribution of *Notomithrax peroni*, Oaro Platform (1976 - 1977).

Table 9.2 Abundance of *Notomithrax peroni* in the study channel, Oaro Platform, December 1976 - December 1977.

Months	Male	Female	Total
December 1976	5	-	5
January 1977	3	3	6
February 1977	5	11	16
March 1977	1	12	13
April 1977	19	21	40
May 1977	14	18	32
June 1977	6	4	10
July 1 1977	6	8	14
July 2 1977	42	120	162
August 1977	22	5	27
September 1977	2	1	3
October 1977	4	3	7
November 1977	5	1	6
December 1977	3	2	5
TOTAL	137	209	346

A comparison of the relative abundance of both species (Fig. 9.6) showed that the ratio of *N. ursus* : *N. peroni* fluctuated closely around 85 : 15 except during (i) late July when it was completely reversed; (ii) August and October when it was 1 : 1; and (iii) November when it was stabilising again. The 85 : 15 ratio seen in September may be an artefact of the extremely low sample size (14 : 3). An examination of the species ratio showed that *N. ursus* outnumbered *N. peroni* by at least 2 : 1 except on three occasions. There were only two months during which the ratio approached unity (Fig. 9.7).

(b) Diurnal Activity of *Notomithrax peroni*

No *N. peroni* were seen out of hiding throughout the sampling period or at any other time except once during May 1977 (7th). On the river side of the study channel (see Plate 3.1) both *N. ursus* and *N. peroni* were observed in a wide channel which had a limestone bottom with many high ridges and few rocks. Algae were sparse, the main species being

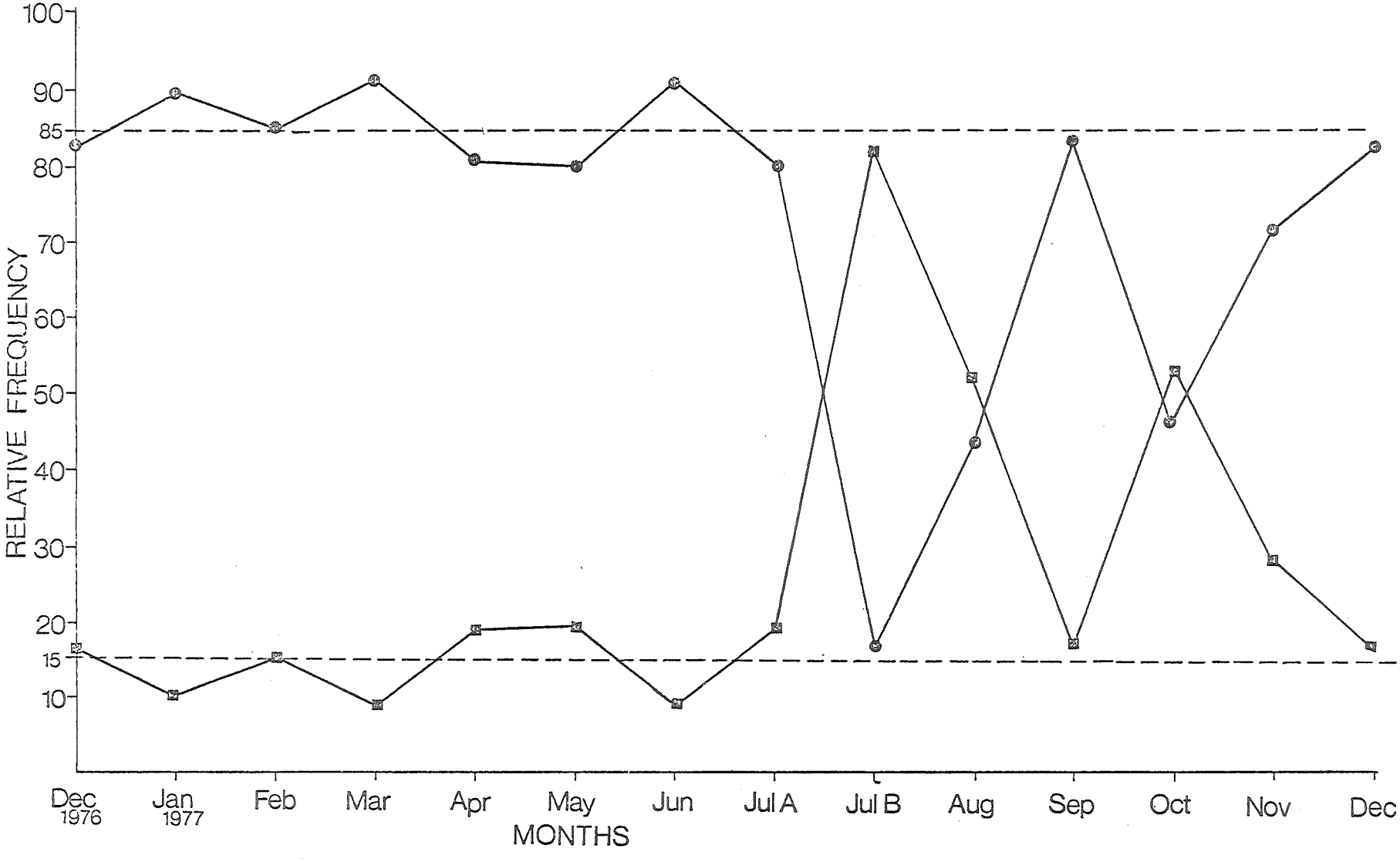


Fig. 9.6 Relative frequency of *Notomithrax ursus* and *N. peroni* in the study channel, Oaro Platform. Squares, *N. peroni*; circles, *N. ursus*.

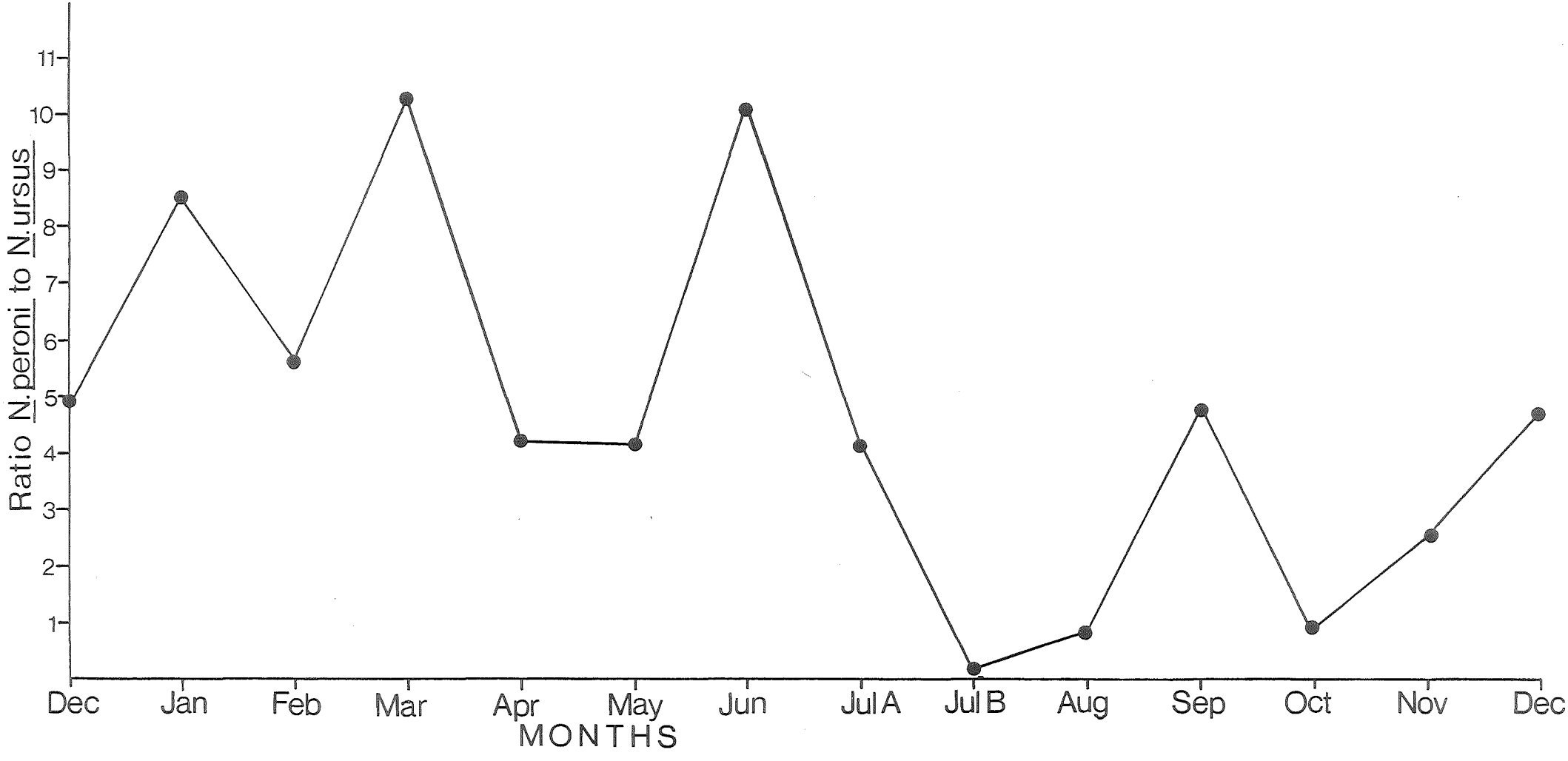


Fig. 9.7 Seasonal changes in the ratio of *Notomithrax peroni* to *N. ursus*, Oaro Platform (1976 - 1977).

Gigartina angulata and *Ulva* spp. The few hiding places available were not occupied and both species were found singly sitting or walking about in direct sunshine. There were more *N. peroni* than *N. ursus* and whereas the *N. peroni* were nearly all female, there were no female *N. ursus*. At any other time during daylight low tides *N. peroni* were anachoretic (i.e., hidden under rocks or in the algae or substrate). Their activity during daylight high tides was not directly investigated. However, in the laboratory holding tanks the occasional motionless crab was observed out of hiding.

Like *N. ursus*, *N. peroni* were active at night. Thirty-five individuals were observed during the night tides (there were seven instances of feeding, thirteen of locomotion and five intraspecific encounters). All 35 individuals were spaced more than five crab lengths apart, but eight had one conspecific and nine had two conspecifics within eight crab lengths. One individual was within eight crab lengths from an *N. ursus* and another was within that distance from two conspecifics and an *N. ursus*.

The four actographs confirmed that *N. peroni* were nocturnal and that, for these crabs at least, like *N. ursus*, an abrupt change in illumination was correlated with a short latency to change activity. In addition there was no suggestion of a tidal component to activity although many more trials would be necessary to confirm this point.

(c) Dispersion of *Notomithrax peroni* Relative to *N. ursus*

The congeneric groups ranged in size from two to twenty-eight crabs. The composition of these groups is presented in Table 9.3. Twenty-one of the forty congeneric groups had an even ratio of the two species and these groups were all of less than five individuals. Of the remaining 19 groups, 15 had more *N. ursus* than *N. peroni*. Of those groups which had more *N. peroni* than *N. ursus*, half occurred in late July when there were many more *N. peroni* than *N. ursus*.

9.3.2 Other Species Found in the Vicinity

The species composition of the Oaro study channel during the day and/or night was diverse (Table 9.4). During daylight low tides *N. ursus* were found in close association with many of these species, in particular sea anemones, tube worms, chitons, *Scutus*, paua, trochids, whelks, mussels,

Table 9.3 Composition of the combined *Notomithrax ursus/N. peroni* groups found in the study channel at Oaro Platform, December 1976 - December 1977.

Months	Groups														
	Even		More *N. ursus* than *N. peroni*								More *N. peroni*				
	1/1	2/2	2/1	2/3	3/1	3/2	6/1	6/2	8/2	9/4	1/2	1/3	2/3	4/24	
December 1976	1		1												
January 1977	2														
February 1977	1				1	1									
March 1977			1				1						1		
April 1977	4	1		2							1				
May 1977	2	2			2				1	1					
June 1977	5				1										
July 1 1977	1														
July 2 1977												1		1	
August 1977								1							
September 1977	1														
October 1977	1														
November 1977			1												
December 1977															
TOTAL	18	3	4	2	4	1	1	1	1	1	1	1	1	1	
GROUP TOTAL	21		15								4				

Table 9.4 Animal species found in the study channel at Oaro Platform, December 1976 - December 1977.

Phylum	Group	Species
Porifera	Sponges	-
Coelenterata	Anthozoa	*Isactinia olivacea* *Isactinia tenebrosa* *Phlyctenactis tuberculosa*
Platyhelminthes	Turbellaria	*Pseudoceros* spp.
Annelida	Polychaeta	*Amphitrite subra* *Pomatoceros carruleus* (syn. *caririferus*)
Mollusca	Amphineura	*Acanthochiton zelandicus* *Amaurochiton glaucus* *Sypharochiton pelliserpentis* *Onithochiton neglectus* *Ischnochiton maorianus*
	Gastropoda	*Cellana ornata* *Cellana radians* *Notoacmea daedala* *Notoacmea helmsi* *Patelloida corticata* *Haliotis iris* *Haliotis australis* *Scutus breviculus* *Melagraphia aethiops* *Turbo smargda* *Microlenchus* spp. *Xymene* sp. *Zeacumantus lutulentus* *Haustrum haustorium* *Cominella maculosa* *Lepsiella scobina* *Buccinulum* spp.
	Nudibranchia	*Ctenodoris flabellifera*
	Pulmonate limpet	*Siphonaria zelandica*
	Bivalvia	*Mytilus edulis aoteanus* *Aulacomya maoriana* *Chione stutchburyi*
	Cephalopoda	*Octopus maorum*

.../Cont'd

Table 9.4 - Cont'd

Phylum	Group	Species
Arthropoda	Chilopodia	*Scolioplanes* spp.
	Crustacea	*Ligia novaezelandiae*
		Paridotea ungulata
		Isocladus armatus
		Alope spinifrons
		Pagurus novaezelandiae
		Pagurus traversi
		Petrolisthes elongatus
		Hemigrapsus edwardsii
		Cancer novaezelandiae
		Halicarcinus spp.
		Notomithrax minor
		Notomithrax peroni
		Leptomithrax longimanus
Echinodermata	Echinoidea	*Evechinus chloroticus*
	Asteroidea	*Asterina regularis*
		Allosticaster insignis
		Astrostole scabra
	Ophiaroiden	*Ophionereis fasciata*
Chordata	Ascidiacea	*Corella eumyota*
	Actinopterygi	*Dellichthys morelandi*
		Tripterygion varium
		Trachelochismus melobesia
		Acanthoclinus quadridactylus
		Pseudolabrus celidotus
		Pseudolabrus luculentus

isopods, the starfish *Asterina*, and several crab species (Table 9.5). Many of these animals are the prey of other related spider crabs (see section 9.1). In contrast there were very few of the potential predators, *Octopus maorum* and *Astrostole scabra*, found in close association with *N. ursus*, and there were no predatory fish seen during daylight low tides. The proportion of the heterospecific potential crab competitors found in close association with *N. ursus* is presented in Table 9.6.

The number of species active at night was small, hermit crabs and fish being the major active species (Table 9.7). Three of the five fish species seen were known predators of crabs in general and two were reported to prey on *Notomithrax* spp.

9.3.3 Field Evidence of Predation in the Field

Only one actual case of predation on *N. ursus* in the field was observed and then the actual capture was not seen. A smallish *Astrostole scabra* was found eating an unmasked male *N. ursus* (CL approximately 20 - 25 mm) at First Bay, Kaikoura Peninsula. When taken from the starfish, this crab was found to be a recently dead individual, not an exuvia or a carapace containing decaying flesh. Consequently, it was in all likelihood actually captured as live prey by *A. scabra*.

During the Oaro field study, 23 *N. ursus* were found which exhibited signs of damage (Table 9.8). Thirteen had a chela missing, one had both chelae missing, two had ambulatory legs missing, and two were without their abdomens. In addition, five *N. ursus* were found which had the dorsum and/or the area between the fourth pair of legs shattered as if 'bitten' or crushed. The damage borne by the 43.2 mm CL male is shown in Plate 9.1a. During general collecting, as well as live crabs, exoskeletons showing this type of damage were frequently found among the intertidal detritus or washed up on the beach (see Plate 9.1b).

9.3.4 Gut Contents of Fish

The guts of 21 moki (*Latridopsis ciliaris*), four Maori chiefs (*Notothenia angustata*), eight yellow-eyed mullet (*Aldreichetta forsteri*), and one butterfish (*Coridolax pullus*) all contained algae, those of two dogfish (*Squalus acanthias*), two rig (*Mustelus lenticulatus*), twelve warihou

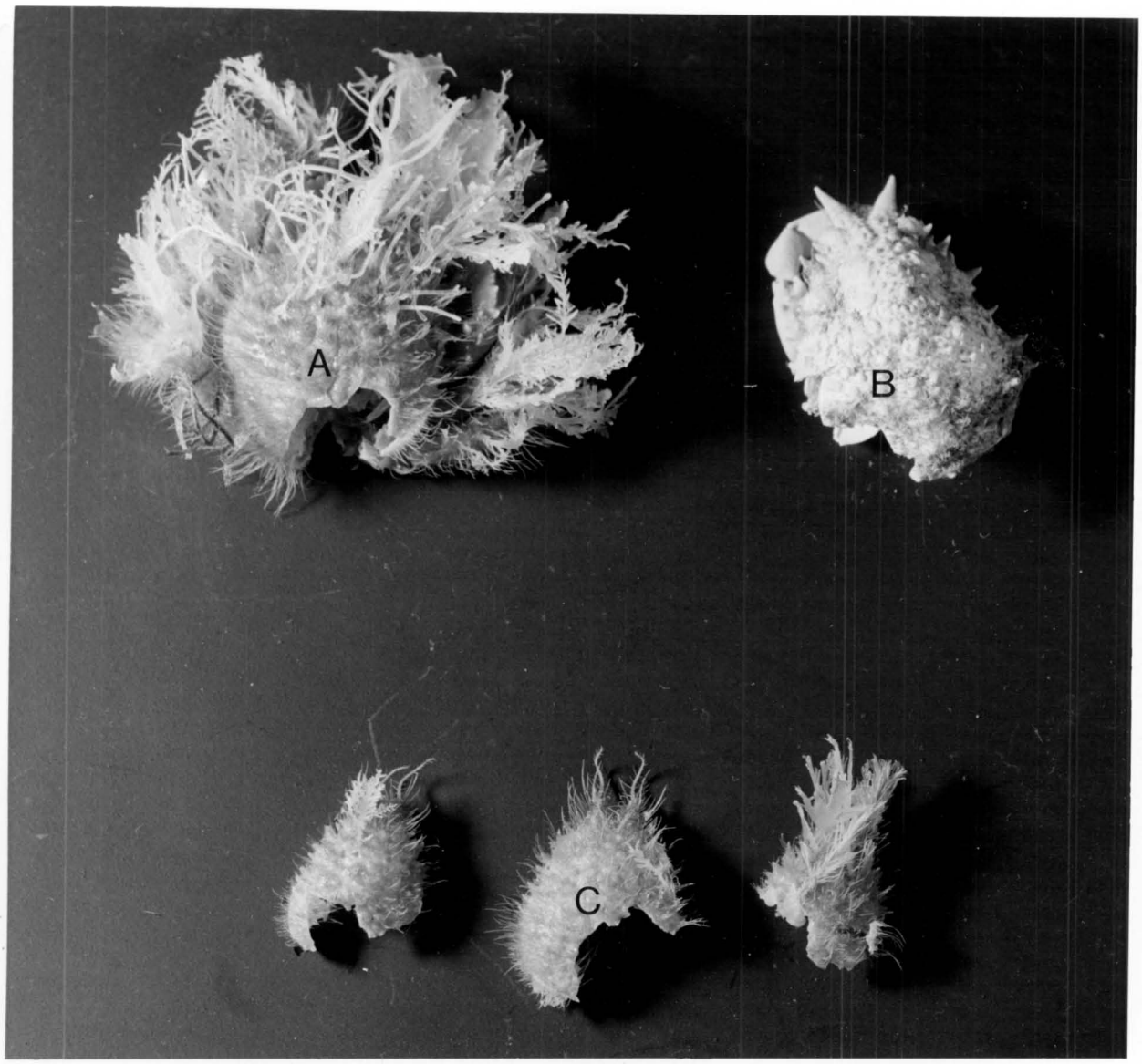


Plate 9.1 Comparison of exoskeletal damage to a live 43.2 mm CL (A) and dead (B) *Notomithrax ursus*, collected from the study channel, with that shown by *N. ursus* bitten by pseudolabrid fish in the laboratory.

Table 9.5 Animal species found in close association with *Notomithrax ursus* in the study channel at Oaro Platform, December 1976 - April 1977.

Phylum	Group	Species	Dec. '76	Jan. '77	Feb. '77	Mar. '77	Apr. '77	Total
Porifera	Sponges	-	-	-	-	2	1	3
Coelenterata	Sea anemones	-	4	4	27	27	22	84
Platyhelminthes	Flatworms	*Pseudocerus* spp.	1	-	-	-	-	1
Annelida	Bristleworms	*Amphitrite rubra*	-	1	-	-	-	1
	Tubeworms	*Pomatoceros caniniferus*	2	18	1	15	20	56
Mollusca	Chitons		22	47	87	116	181	453
	Limpets		3	4	9	1	3	20
	Paua spp.	*Scutus* spp.	5	2	5	12	28	52
		Haliotis spp.	3	17	29	27	28	104
	Trochids	*Turbo* spp.	13	30	27	32	39	141
		Zeacumantus spp.	-	30	40	81	120	271
		General	11	-	-	-	-	11
	Whelks		13	33	58	84	79	267
	Nudibranchia		-	-	1	-	-	1
	Bivalves	General	7	-	-	-	-	7
		Mussels	-	4	21	4	18	47
		Cockles	-	-	-	-	1	1
	Cephalopods	*Octopus maorum*	1	-	1	-	-	2

.../Cont'd

Table 9.5 - Cont'd

Phylum	Group	Species	Dec.'76	Jan. '77	Feb. ' 77	Mar. '77	Apr. '77	Total
Arthropods	Centipedes		-	-	-	-	1	1
	Isopoda	*Ligia* spp.	2	-	5	-	-	7
		Paridotea ungulata	1	-	-	-	-	1
		Isocladus spp.	-	-	1	-	22	23
	Prawn	*Alope spinifrons*	-	-	1	-	-	1
	Hermit Crabs	*Pagurus* spp.	12	10	37	55	102	216
		Petrolisthes elongatus	20	47	69	102	133	371
		Hemigrapsus edwardsii	10	-	-	-	-	10
		Cancer novaezelandiae	1	-	-	-	-	1
		Helicarcinus spp.	-	-	-	6	3	9
Echinodermata		*Evechinus* spp.	-	1	5	6	6	18
	Starfish	General sp.	1	-	-	-	-	1
		Asterina spp.	12	4	12	28	25	81
		Astrostole scabra	2	-	2	2	4	10
Chordata	Ascidians	*Corella eumyota*	15	-	9	4	4	33
	Fish	*Dellichthys morelandi*	1	3	-	2	1	7
		General sp.	-	-	-	10	8	18

Table 9.6 The proportion of other crab species found with *Notomithrax ursus* in the study channel at Oaro Platform, December 1976 - April 1977.

Species	Dec. '76	Jan. '77	Feb. '77	Mar. '77	Apr. '77	Total (%)
Pagurus spp.	22.64	17.54	34.9	33.74	42.86	35.58
Petrolisthes elongatus	37.74	82.46	65.09	62.58	55.88	61.12
Hemigrapsus edwardsii	18.88	-	-	-	-	1.65
Cancer novaezelandiae	1.89	-	-	-	-	0.16
Halicarcinus spp.	-	-	-	3.68	1.26	1.48

Table 9.7 Animal species observed to be active at night in the vicinity of *Notomithrax ursus* and *N. peroni*.

Species	19/10/77	12/11/77	14/11/77	5/2/78	6/2/78	7/2/78	22/2/78	Total
Turbo smargda		x						1
Alope spinifrons				x		x	x	3
Pagurus spp.	x	x		x	x	x		5
Petrolisthes elongatus					x	x		2
Acanthoclinus quadridactylus	x		x	x	x	x		5
Pseudolabrus celidotus		x	x					2
Pseudolabrus luculentus		x						1
Dellichthys morelandi			x	x				2
Tripterygion varium	x		x	x				3

Table 9.8 *Notomithrax ursus*, bearing signs of physical damage, found in the study channel at Oaro Platform.

Month	Sex	Size (mm)	Maturity	Type of Damage
January	F	22.7	J	B5 - damaged as if bitten
	F	22.8	J	B5 - damaged as if bitten
February	F	27.6	J	Regenerating all right ALs
March	F	27.7	J	LC - missing
	F	29.8	J	Telson missing
	M	21.1	J	B5 - broken as if bitten
	M	27.3	J	RAL4 regenerating
April	F	28.0	J	RC - missing
	F	38.0	A	RC - missing
	M	28.5	J	LC - regenerating
	* M	43.2	A	Dorsum 'bitten' on right-hand side
May	F	28.2	A	Very back of dorsum been chipped away
	F	29.9	A	LC - missing
	M	21.6	J	LC - propodus had large dent in it
	M	27.9	J	LC - missing, telson broken
	M	46.8	A	RC - missing
June	F	-	A	LC - missing
	M	41.8	A	RC - missing
July	M	27.1	J	LC - missing
August	F	-	A	LC - missing
	F	28.5	A	LC - missing
	M	33.3	?	LC and RC - missing
September	F	25.5	A	LC - missing

* See Plate 9.1A

Key: B5 - rear of dorsum between AL4's
AL - ambulatory leg
C - cheliped
L - left
R - right
J - juvenile
A - adult

(*Seriolella brama*), one scorpion fish (*Scorpaena cardinalis*) and four paketi (*Pseudolabrus celidotus*) all contained Crustacea, especially *Munida*, but no *Notomithrax* spp.

9.3.5 Predation Experiments with Fish

The results from the 13 fish tested are presented in Table 9.9. *Scorpoena cardinalis*, *Latridopsis ciliaris*, *Helicolenus papillosus*, and *Haplodactylus meandrus* all refused to eat *N. ursus* even after several days of food deprivation. *S. cardinalis* was observed to suck in an unmasked male *N. ursus* and then to spit it out immediately. The six pseudolabrids consumed four masked and five unmasked *N. ursus* and attacked two further masked crabs. Both of these were attacked from behind and while one escaped, leaving the fish with a mouthful of algae, the other had its carapace bitten through. The remains of several *N. ursus* also showed these bite marks (see Plate 9.1c) which were of the same type as those found on crabs in the field. At the end of the experiment the gut contents of *Pseudolabrus fucicola* and *P. celidotus* were examined and both contained very definite *N. ursus* remains.

9.3.6 Predation Experiments with *Astrostole scabra*

Over six days the 15 *A. scabra* consumed three masked and five unmasked of the original eight masked and eight unmasked crabs. One *A. scabra* (size 97.7 mm) was actually observed to 'capture' an unmasked juvenile female *N. ursus* (CL 15.8 mm). As the starfish moved along, the crab was contacted by the tip of an arm. The starfish then continued on until its 'stomach' was directly over the crab, then stopped and egestion began.

9.3.7 Predation Experiments with *Octopus*

The small *Octopus maorum* hunted and readily ate Crustacea in captivity. The number of animals eaten from those available for all the species which were offered is shown in Table 9.10. Behavioural observations showed that *Hemigrapsus crenulatus*, *Helice crassa*, and *Pinnotheres novaezelandiae* were readily captured and all were consumed. Although it pursued all five of the shrimps (*Alope spinifrons*) the octopus only managed to capture two. The octopus did not appear to

Table 9.9 Laboratory predation of *Notomithrax ursus* by fish.

Tank	Species	Common Name	Length from snout - caudal fork (cm)	CL Size (mm) *Notomithrax* Masked M	Masked F	Unmasked M	Unmasked F	Test Duration (days)	Eaten
1	*Scorpoena cardinalis*	Scorpionfish	20	18.0	18.0	18.7	20.0	6.5	Nothing eaten
2	*Latridopsis ciliaris*	Blue Moki	16	10.2	14.8	11.0	16.7	5.5 (died)	Nothing eaten
			17	14.9	17.0	16.3	18.8	6.5	Nothing eaten
3	*Helicolenus papillosus*	Banded Sea Perch	30	21.1	21.9	20.9	21.1	6.5	Nothing eaten
4	**Pseudolabrus fucicola*	Banded Parrotfish	20	18.3[E]	19.3	21.8[E]	19.3		1 eaten after 3 days
			22	20.7	18.3	21.4	17.5	6.5	3 eaten after 6.5 days
			23	18.1[E]	17.8[E]	19.2	20.3		
1	***Pseudolabrus celidotus* (pre-starved 7 days)	Spotty	25.5	19.3[E]	19.5[D]	21.5[E]	19.4[E]	1	3 eaten, 1 damaged
2	*Haplodactylus meandratus* (pre-starved 7 days)	Marblefish	34	24.6	22.0	24.0	20.6	1 (died)	Nothing eaten
1	†*Pseudolabrus celidotus*	Spotty			21.4		21.2	1	Nothing eaten
2	†*Pseudolabrus miles*			18.4[A]			18.5[E]	1	Unmasked eaten
3	†*Pseudolabrus fucicola*			18.7[P]			21.2[E]	1	Unmasked eaten
				18.4		18.7		1	Unmasked eaten
4	*Scorpeona cardinalis*	Scorpionfish		21.1		22.2[S]			Nothing eaten

* Gut contents examined, one contained legs, carapace and chelae of *N. ursus*.
** Gut contents examined contained very definite *N. ursus* remains.
† Watched behaviour.

A = algal autotomy; D = carapace bitten through; E = eaten; P = partly masked by end of trial - algal autotomy;
S = sucked in then spat out.

Table 9.10 The number and type of animals offered to a captive *Octopus maorum* and subsequently eaten by that octopus.

Species	Total Number	
	Offered	Eaten
Petrolisthes elongatus	9	5
Hemigrapsus crenulatus	39	39
Helice crassa	9	9
Pinnotheres novaezelandiae	2	2
Notomithrax ursus - unmasked	9	5
Notomithrax ursus - masked	7	1
Notomithrax peroni - masked	2	0
Alope spinifrons	5	2

experience any difficulty in capturing the remaining species; however, they were not attacked as readily. In fact, the octopus showed differential predation between crabs which had an algal mask and those which did not. Only one masked crab was accepted and in that instance the crab walked into the octopus who was nine days food deprived.

9.4 DISCUSSION

Although of a preliminary nature, the results gained from the investigation into the other species sharing *N. ursus*'s habitat were sufficient to answer the questions posed at the beginning of this chapter.

N. peroni was present in the channel throughout the whole year and, like *N. ursus*, was nocturnally active. In addition, the intraspecific and intrageneric spacing for both species was the same at about five crab lengths. For most of the year the ratio was 85 *N. ursus* : 15 *N. peroni*, but in August and October the ratio changed to 1 : 1. It is possible that the algal mask of both species is effective enough to tolerate a 1 : 1 ratio, especially as the combined population of both species during these two months is small, allowing greater dispersion. But in late July the combined population exhibited a complete reversal to 15 *N. ursus* : 85 *N. peroni*. Examination of abundance of both species shows that when the frequency of one species increased, that of the other decreased. When *N. ursus* peaked in April (170) there were few *N. peroni* (40), and when *N. peroni* peaked in late July (240) there were few *N. ursus* (34). The highest number of animals recorded in the channel was 274. *N. peroni* had a peak in the relative abundance of ovigerous females a month prior to that of *N. ursus*. Both species migrated inshore to brood (and breed?) so this difference in proportion of ovigerous females also suggests that the joint population of *N. ursus* and *N. peroni* may be density dependent.

The facts that the combined density of *N. ursus* and *N. peroni* was stable and that not all the available shelter was utilised suggest that the combined density was a function of spacing out to maintain crypsis. In turn one would expect spacing out to be achieved by some form of inter-specific agonistic behaviour - an hypothesis that was supported by casual laboratory observations at least.

The list of other species present in the channel shows that there were plenty of prey available and many of these animals were, in fact, eaten by related spider crabs (section 9.1). Thus, *N. ursus* is not a non-hunter through any absence of suitable prey species. Even if *N. ursus* does hunt, and I never managed to observe it, very few of the species present in the habitat had the sensory capabilities which would require *N. ursus* to be cryptic.

Five crab species as well as *N. peroni* were present in the channel with *N. ursus*. All these species, but particularly *N. peroni*, could be competitors of *N. ursus* for food, space and shelter. It is generally accepted (Curio, 1976) that when given a choice of prey, predators will hunt first those animals which require the least output of energy or those which give the greatest energy yield. When *Hemigrapsus edwardsii*, *Petrolisthes elongatus*, *Cancer novaezelandiae* and *Halicarcinus* spp. are exposed in the field, their general appearance and behaviour make them far more apparent to the human eye than masked *Notomithrax*. Visually oriented predators would be more likely to be attracted to these species and consequently more likely to attack them rather than more cryptic prey. Hence, these other non-masking crabs may dilute the effect of predators on *N. ursus*. By virtue of their gastropod shells, the *Pagurus* spp. would be harder to capture than the other non-masking species so these hermit crabs may not dilute the impact of predators to the same extent. However, any choice of edible prey must cause some dilution of the effect of predators. The preliminary observations with the octopus did show that the more conspicuous species of crab offered were more readily and rapidly attacked.

The list of the other species revealed that of the reported predators of *N. ursus* only *Astrostole scabra*, *Octopus maorum* and two *Pseudolabrus* species were present in the study channel. However, the other reported predators were present around Kaikoura and may feed on *N. ursus* in deeper water.

The random analysis of gut contents failed to find any evidence of predation of *N. ursus* by feral fish. However, in the case of carnivorous species this was in all probability due to the extremely small sample size. As *N. ursus* remains were quite unmistakable in the gut contents of the captive fish, it is unlikely that their remains were missed in feral fish.

Laboratory experiments demonstrated that in the absence of other prey, captive *Astrostole scabra* certainly ate *N. ursus* regardless of the algal mask. However, these starfish were not considered to be important predators of *N. ursus* as they appeared to graze over the crabs. In addition, Town (1979) found that in the Kaikoura region at least, crabs in general formed a very minor part of the diet of *A. scabra*.

Species that exploit the same class of environmental resources in a similar way are grouped into 'guilds' (Root, 1967) and the fish reported to prey on *N. ursus* all belong to the 'bottom stalkers' guild. In New Zealand the majority of the bottom stalkers guild are nocturnal (Doake, 1972) so they are suitable predators of *N. ursus*. However, the only captive nocturnal bottom stalker tested (*Helicolenus papillosus*) refused to eat *N. ursus*. Laboratory experiments did, however, confirm that *Pseudolabrus celidotus* and *P. fucicola* ate *N. ursus* as did the hitherto unreported *P. miles*. The Labridae are diurnal bottom stalkers so one would not expect them to prey upon the diurnally anachoretic *N. ursus*. However, many diurnal bottom stalkers capitalise on the fact that hidden species are frequently driven from cover when the habitat is disturbed. The Labridae in fact feed by flushing the crabs out of cover (Hobson, 1968). Consequently, the mask is unlikely to function as crypsis against labrid fish. Observations of the captive labrids revealed that they grabbed at *N. ursus* and the injuries sustained by the crabs were the same as those found on *N. ursus* in the field, corroborating the reports that *Pseudolabrus* spp. are feral predators of *N. ursus*. Also, one *N. ursus* managed to escape leaving the fish with a mouthful of algae. This isolated case may be more prevalent in the field where *N. ursus* has the advantage of algal clumps which will serve to disorient the fish's grab. Consequently, it is possible that the algal mask functions by defence autotomy against fish which grab at prey.

The 'bite' marks were found only on the rear of the carapace, suggesting either that the predators attack only from above and behind, or that they bite any body part, but algal autotomy is very efficient at the front of the crab where the longest and greatest number of algal pieces occur. The number of feral crabs found, of all classes, which lacked chelipeds and legs, which are not as heavily masked as the body, supports the latter postulate.

In conclusion, the results suggest that the mask is an anti-predator device which may function as a defence autotomy against labrid fish and/or as crypsis against octopuses and nocturnal bottom stalking fish.

SECTION I

CHAPTER 10

DISCUSSION

Systematic field and laboratory observations and experiments generated data which have contributed to answering the five questions posed in the introduction to this section.

10.1 THE MASK AS AN ADAPTATION

The apparent lack of inter-individual variability in the number of algal pieces used in the mask and their pattern of application between the different sex, size, and maturity classes of *Notomithrax ursus* suggested that masking behaviour is not a pleiotrophic effect. Rather, masking seems to be directly subject to strong selection pressures. This hypothesis was supported by the amount of time and energy *N. ursus* invested in forming and maintaining a mask. Masking behaviour was exhibited by the smallest crabs found and was continued throughout the entire life by both sexes. Masking behaviour was accorded top priority over other maintenance behaviours. Both moulted crabs and those otherwise deprived of their mask replaced it as soon as they were physically able. Field study indicated that the algal mask would probably only be of use when *N. ursus* was not anachoretic. Johnson (1976) held that selection pressure is likely to be intense if a complex adaptation was operative for only short periods of an animal's life. Since *N. ursus* is anachoretic for the majority of the time, the hypothesis that the mask is subject to intense selection is further supported.

10.2 THE MASK AS CRYPSIS

The harmony achieved between the illusory form, provided by the attributes of the mask itself, and the total behavioural repertoire of individual, intra and interspecific behaviours, provided strong support for the hypothesis that the mask functions as crypsis.

Although *N. ursus* did not always exactly match its background, it generally blended with the surroundings by virtue of the fact that the materials used in the mask were taken from the immediate environment of the crab. The continual replenishment of the mask also enables *N. ursus* to blend, at least partially with the immediate background without restricting its freedom of movement. Further, the variability in appearance among individuals, and also of the same individual at different times, caused by this continual replenishment of the mask, may hamper the formation of a search image by predators. The use of a commonly occurring material such as algae, coupled with the habit of being closely associated with the algae, provides the predator with many more non-rewarding encounters with a non-edible object before encountering an edible crab. This situation may then result in the predator ceasing to search as it has either habituated to the algae or confused *N. ursus* with the inedible.

The crab was rendered cryptic not only by the fact that the material came from the background but also by the resultant shape of the mask. The longest algal pieces were attached to the rostral area so that they pointed anteriorly. These anterior pieces gave the crab a very elongated, uncrab-like shape. In addition, these algal pieces covered the unmasked, coloured and hence visually conspicuous, chelipeds and oral region. The rostrum and anterior legs had the highest probability of being masked, supporting the hypothesis that the mask served these additional functions. With the exception of the very rear of the crab, the greater the amount of sharply defined outline of a body area, the greater the probability that the area will be masked. Consequently, the mask may function to obliterate the body contours rather than to hide the animal completely.

To maintain crypsis, an animal should not move, especially during daylight, if the predator is visually oriented. Indeed, *N. ursus* is not only nocturnally active, but even then is only exposed when necessary. The majority of the time *N. ursus* were anachoretic. *N. ursus* were extremely photonegative and their activity was controlled by changes in illumination. If disturbed, *N. ursus* immediately sought cover, and in the absence of cover, they tried to bury themselves. Excavating behaviour occurred during periods of illumination and only during darkness in the presence of predator-like stimuli. This indicates that *N. ursus*

are more vulnerable to selection, presumably from predators, during daylight. *N. ursus* exhibited a preference for hiding under rocks rather than under the algae or in the substrate during periods of illumination.

During brief periods of exposure at night, *N. ursus* were dispersed, 68% being greater than 100 cm (*ca.* 33 crab lengths) from a conspecific. Generally, *N. ursus* avoided one another, but the males displayed when within 4 - 5 crab lengths of each other. The maintenance of such large inter-individual distances between non-anachoretic crabs suggests that spacing is important to these crabs. Spacing appeared to be achieved by agonistic behaviour and large inter-individual distances were possible as only a small portion (14%) of *N. ursus* was active at any one time. As *N. ursus* were never inactive when exposed, the mask may function as crypsis to enable the performance of those behaviours, such as feeding, which conflict with their anachoretic behaviour.

The results from the field dispersal study, coupled with those from the laboratory activity study, revealed that *N. ursus* made large-scale movements at night. Since few crabs were exposed, this movement must occur under the cover of algae and through hidden rock crevices. This large-scale cryptic movement suggests that the selection pressure is predatory and their photonegative responses further indicate that at least one of their nocturnal predators is visually oriented. However, the mask may also function against the chemical, tactile, and auditory senses of other nocturnal predators.

Even when on an appropriate background, a cryptic animal may still be conspicuous if it does not assume an appropriate resting attitude. When at rest, *N. ursus* sat with the limbs adducted and the body oriented forward so that the unmasked body parts were hidden by the masked areas. If on a horizontal surface, *N. ursus* did not display a consistent alignment with their background. This is not surprising in view of the complexity and changeable nature of both the algal mask and the background of *N. ursus* and the fact that, when exposed, *N. ursus* were active rather than motionless. *N. ursus* did, however, consistently rest posterior end uppermost when on vertical surfaces. This behaviour appeared linked with preventing the anterior portion of these animals from being unduly highlighted with respect to the light source.

There are times when *N. ursus* must move away from cover, but even then its very slow, deliberate movement and its habit of climbing over the algae also seem conducive to concealment. Further, when exposed to an aversive stimulus while walking, *N. ursus* froze. Freezing following locomotion is probably of great importance since movement may prove fatal.

In addition, *N. ursus* was observed to display a repeated anterior-posterior rocking motion after it has come to rest, especially if preceded by a disturbance such as the proximity of a predator or prodding by a human. To a human observer, this rocking motion is reminiscent of the 'wafting' motion of algae caused by water currents. Rocking may function to confuse a predator that has previously detected linear movement, which has suddenly become lost amongst the irrelevant background. Certainly, Robinson (1969) demonstrated that predatory tamarins (*Saguinus geoffroyi*) were more responsive to straightforward linear movements than to rocking movements. If this unresponsiveness also occurs among the predators of *N. ursus*, then it follows that *N. ursus* could increase the effectiveness of their rocking movements by orienting so that the longitudinal axis of the body is in line with the prevailing water currents. This aspect would be a worthwile one to test experimentally. A sideways rocking was occasioned during excavating and this motion may also serve to conceal the comparatively gross movements involved in excavating.

Many of the secondary defences exhibited also seem correlated with maintaining crypsis. Trapping the stimulus between the lateral spines and the first legs (AL1 pinch) may have a startle effect. The same result may be achieved by both autotomy of the limbs, and 'autotomy' of the algae. In all three cases, the predator has to relocate the prey. Limb extension rendered the crabs difficult to handle. Finally, flexion appeared to have several uses. The lack of movement may well inhibit the release of the attack response by predators or it may cause a relaxation of attention by the predator, giving the crab a chance to escape. Since the legs are also masked, flexion may change the crab's form sufficiently to confuse the predator. Flexion also conceals the contrasting ventral marking. If the predator does attack, the vulnerable areas of the crab are protected and the predator also lacks easy ways of holding the prey. It may be noted here that flexion behaviour appears identical with similar behaviours

reported in other animals. Edmunds (1974) terms this flexion and subsequent freezing behaviour 'thanatosis', i.e., death feigning. If flexion and thanatosis are one and the same behaviour (as they appear to be) then the term thanatosis is a misnomer as in death animals do not hold stereotyped positions; they either go limp or *rigor mortis* results in very unnatural positions being held. The term catalepsy (Godden, 1974) appears far more accurate. However, 'flexion' is probably the most suitable word as it describes the behaviour as well as naming it.

The mask was not involved with intraspecific behaviours concerned with breeding. However, it was related to size. Smaller crabs were more heavily and more consistently masked, in terms of both the areas covered and the average number of algal species applied/segment. In addition, juvenile crabs used more species of algae than adults. Since smaller, younger animals are generally more vulnerable, the mask may be involved in protection against other animals.

The agonistic behaviour of *N. ursus* was related to the illumination cycle. *N. ursus* were non-aggressive and often aggregated during periods of illumination, when they seemed most conspicuous. However, males could be highly aggressive at night when they seemed least conspicuous. Huntingford (1976) hypothesised that social aggression is rare when predator pressure is high, suggesting that *N. ursus* is subject to high predation pressure at least during the day.

10.3 IS THE MASK ANTI-CRYPSIS OR PROCRYPSIS?

There was no evidence from field or laboratory studies that *N. ursus* were active predators. Consequently, the hypothesis that the mask functions as anti-crypsis to deceive potential prey can be dismissed. Hence the mask most probably functions as procrypsis.

10.4 WHICH SPECIES ARE POTENTIAL PREDATORS OF *N. URSUS*?

Although *N. ursus* is anachoretic for the majority of the time, it still undergoes relatively large-scale daily and seasonal migrations. Consequently, *N. ursus* may be exposed to predation during this movement.

Since *N. ursus* is nocturnally active, it is most likely to be preyed upon by a nocturnal predator.

Astrostole scabra, *Octopus maorum* and two *Pseudolabrus* spp., which are reported to prey upon masking crabs, were found at all collecting sites. However, the only direct evidence of predation in the field was one observation of *A. scabra* devouring a masked *N. ursus*. *N. ursus* only constitute a minor part of the diet of *A. scabra* (J. Town, pers. comm.) and preliminary observations of their interactions suggested that *N. ursus* were grazed rather than hunted.

The literature revealed 13 species of fish with *N. ursus* in the gut, the most important of these being the pseudolabrids and the blue cod. These fish were reputed to be diurnally active, whilst *N. ursus* is anachoretic during the day. However, labrids feed by flushing crabs out from cover. *N. ursus* secures itself to the rocks and algae by a powerful grip. This gripping probably further increases their inaccessibility to fish, who lack the morphology necessary to prise objects out of crevices. However, some *N. ursus* found in the field showed damage to the posterior part of the body. This damage was the same as that inflicted on laboratory *N. ursus* by predatory pseudolabrids, indicating that these fish may be natural predators of *N. ursus*. Furthermore, one crab was observed to escape predation, leaving the fish with a mouthful of algae. This isolated case suggests that the mask may well alter the fish's perception of the crab's body outline, the predatory fish mistaking the edge of the mask for the edge of the body. Consequently, the fish snaps at *N. ursus* too soon, grasping only the algae which can be 'autotomised'. However, owing to the differing activity patterns of these two species, fish probably do not exert a strong selection on *N. ursus*. Therefore, this 'defence autotomy' is probably a secondary function of the mask.

Octopuses are reported to be the major predators of several majid species. As the remains left after a crab has been eaten by an octopus are the same as those left by a moulted crab, and both octopus and crabs are nocturnal, direct evidence in the field was difficult to obtain. Octopuses were present in the intertidal area during summer when the intertidal *N. ursus* population was composed of young, small crabs. In addition, since moulting occurred over this time, unmasked

individuals were present in the intertidal area as well. Several newly hatched species of cephalopods have been found to respond only to crab-shaped prey images. This response is modified to include other shapes as the individuals grow. If New Zealand octopuses are natural predators of *N. ursus* and the young octopuses do have a crab-shape prey image, it would be advantageous for juvenile *N. ursus* to be heavily masked as soon as they settle.

10.5 CONSIDERATION OF OTHER FUNCTIONS

Although a signalling function cannot be discounted, no evidence was found to support this hypothesis.

N. ursus were able to perceive and respond to visual, chemical and tactile-vibratory stimuli. Also, these crabs were able to differentiate between classes of conspecifics. However, the presence or absence of the algal mask had no effect on the response of *N. ursus* to conspecifics of any class. This indicated that the mask was unlikely to have an intraspecific signalling function, nor is it likely that it is used as an assessment cue of fighting ability. If the mask is used in courtship or in agonistic encounters, some sex, maturity, size or seasonal differences in the amount or type of materials applied would be expected. The mask shows none of these.

Since *N. ursus* were so closely associated with the algae, and they were only exposed at night, the algal mask was not conspicuous, hence it was also unlikely to be an interspecific signal (e.g., aposematism). For an aposematic function, strong evidence that *N. ursus* was noxious or physically dangerous to a potential predator would be necessary. However, laboratory studies revealed no evidence of this. The octopus, fish, and starfish predators showed no reluctance to attack and eat *N. ursus* once they had detected these crabs. If the mask was an anti-predator signal, one would expect that one particular alga would be more conspicuous and hence favoured over other species. However, *N. ursus* used a variety of species of algae in a multitude of combinations. The 'choice' of algae used appeared to be governed solely by which materials were present in the environment.

On the basis of the foregoing arguments, it would seem that if the mask does have a role in communication it is at most secondary.

Furthermore, predators would seem to be the major selection pressure contributing to the evolution of masking.

The role of the mask as a supplementary food source can also be eliminated as there was no evidence that *N. ursus* is herbivorous. Even if *N. ursus* were herbivorous, the benefit accruing from storing food on its back, when it lives amongst such a plentiful supply of potential food, would be difficult to understand. Certainly much of the material that is applied (e.g., shell chips), when algae is also present, is inedible. Also, masking was not inversely correlated with the amount of environmental algae available which might be expected if food was being stored. In deeper water, where algae were scarce, *N. ursus* applied very little algae. In addition, some algae would surely have more nutritional value than others, but *N. ursus* used anything that it could cut and apply. Finally, if the mask is a food supply, why are the pieces applied in such a stereotyped elaborate pattern?

10.6 REQUIREMENTS FOR KEEPING *N. URSUS*

The results from this study also provided some valuable information on the requirements necessary to keep *N. ursus* successfully in the laboratory. Since these crabs were anachoretic, the aquaria must be equipped with hiding places, especially rock cover. Their lack of substrate preference means that bare concrete bases will be sufficient. However, if excavating behaviour is to be studied, the tanks will need to be equipped with a particulate floor. Pea gravel is the most suitable as it enables more efficient tank cleaning than substrates with finer particles. As *N. ursus* dispersed during their active phase and showed aggressive behaviour when closer to each other than 12 - 15 cm, the number of crabs kept/tank should allow about 100 - 144 cm^2 floor space/crab. The lack of a tidal rhythm exhibited by *N. ursus* meant that it is not necessary to provide tidal fluctuations in the aquaria. Finally, as these crabs were exposed at night, any experiments and observations concerning the function of the mask should be conducted in darkness or at least in very dim conditions.

- - -

The data presented in this section strongly support the hypothesis that masking is a specific adaptation and that predators were the major selection pressure responsible for its evolution. However, these data do not reveal the nature of the advantage conferred by masking. This question will be investigated in the next section by means of experiments that compare the survival of masked and unmasked *N. ursus* exposed to a probable natural predator.

SECTION II

LABORATORY STUDY OF THE EFFECTIVENESS OF THE MASK

SECTION II

CHAPTER 11

INTRODUCTION

Data collected in Section I of this thesis suggested that the function of the algal mask of *Notomithrax ursus* was most likely procrypsis. However, as explained in Chapter 1, it is not sufficient to demonstrate a functional design. One should also provide experimental evidence that the character under investigation performs the function which the hypothesis demands of it.

Since the 1880s there has been considerable work concerning the effect of concealing colouration in protecting animals from predators and prey (Poulton, 1890; Cott, 1940; Friedmann, 1944; Breder, 1946; Edmunds, 1974). Furthermore, it is generally agreed by biologists that natural selection must play an important role in the evolution of protective colouration. However, there have been relatively few experiments testing the efficacy of selective agents assumed to be responsible for shaping these adaptations. This is especially true of animals, such as masking crabs, which derive their supposed anti-predatory protection by the utilisation of adventitious materials. Evidence demonstrating the effect of defensive adaptations (especially protective colouration) on survival in other species has been the subject of experiments by Poulton (1887), di Cesnola (1904, 1907), Sumner (1934, 1935a, b), Carrick (1936), Isley (1938), Popham (1941), Dice (1947), de Ruiter (1952, 1956), Blest (1957), Kettlewell (1955, 1956, 1958, 1961), Tinbergen *et al.* (1962), Clarke *et al.* (1963), Baker (1970), Kaufman (1973) (see Edmunds, 1974 for additional references).

Poulton (1887, 1890, 1908, 1932) devoted a great deal of time to the study of adventitious use and he provided convincing theoretical arguments (based on comparative and contextural information) for the efficacy of this behaviour in concealing the possessor from its predators or prey. However, the few experiments he presented suffered from inadequate sample sizes. Although Wicksten (1980) reported that the mask was effective against predatory fish, octopuses and the sea

otter, there is no experimental, or other detailed, evidence in the literature to support the hypothesis that the mask is an advantage against predators. Consequently, the major aim of the research presented in this section was to provide experimental evidence that the mask was advantageous for the survival of *N. ursus* against predators.

Typically, an experiment testing the advantage of a character (i.e., a selection experiment) involves the establishment of two groups, the character in question being present in one and absent in the other, with all other conditions equal. The investigator subjects the two groups to the supposed situation of selection and compares survival. In the present case, this meant that the encounters between *N. ursus* and their natural enemies had to be observed to determine whether the predators were less likely to prey upon masked specimens, than individuals that lacked the adventitious algal mask, but were entirely similar in all other respects.

When examining the function of a character (e.g., a behavioural or morphological attribute) it is the differences in this character that are of concern. In other selection experiments, this has raised a practical problem. Very few of the species studied have been polymorphic for the character under investigation. The most notable exception being Sheppard's (1951) study on the differential survival of the yellow, pink and brown morphs of the banded snail, *Cepaea nemoralis*. Hence the animals have to be tampered with to obtain a difference, and the morphs so obtained are often very unnatural. For example, Benson (1972) painted the wings of the butterfly *Heliconius erato* to obtain a difference. Changes of this type (i.e., in external morphology) are liable to have associated cue changes (e.g., the odour or reflectance of the paint) confounding the reasons for the lowered survival of the test animals. As the majority of an organism's characters are genetically linked with other characters, a natural change in a character usually involves corresponding differences in these other associated characters. There is no guarantee that any observed lowering of fitness is the result of increased susceptibility to predation as to any other selection pressure. For example, in *Cepaea nemoralis* the unbanded snails are more resistant to heat than are banded snails, and there are also behavioural differences associated with the different *Cepaea* morphs. De Ruiter (1955) studied the function

of the countershading character in stick caterpillars (Sphingidae). He produced his 'morph' by using normal and inverted caterpillars. However, de Ruiter was comparing absence of a shadow with exaggerated shadow, not absence with normal, or exaggerated with normal. Masked and unmasked morphs involve a comparison of normal with the absence of the character.

Since *N. ursus* gain their character (the algal mask) adventitiously, an associated physiological change between masked and unmasked individuals is very unlikely. Furthermore, the results presented in Section I demonstrated that careful removal of the algal mask did not cause any evident differences in behaviour between the two 'morphs'. Finally, unmasked crabs occur naturally in the field during the moulting season. Consequently, masking is a particularly suitable character with which to demonstrate the advantages of protective colouration.

To be valid, a selection experiment must satisfy certain criteria. The unattainable ideal would be to have a detailed knowledge of the numbers and character states of the species concerned available to predators under natural conditions, over a wide area for a long period of time. In addition, large numbers of both predators and prey should be utilised. Unfortunately, these methods often prove impracticable and the majority of published selection experiments fall far short of the ideal (for discussion of this issue, see Popham, 1941; Robinson, 1969; Edmunds, 1972, 1974; Emlen, 1973; Johnson, 1976). The majority of selection experiments can be criticised for having too small a sample size or because predation was inferred, but not actually observed (e.g., Clark *et al.*, 1963). For example, Baker (1970) found that hailstones and not predators were responsible for the cabbage butterfly *Pieris rapae* depositing its cryptic eggs underneath leaves. In addition, many of the studies have not excluded the other reasons for differential predation. For example, the wasp *Vespula vulgaris* was shown to react to the difference in haemolymph between the green and yellow morphs of *Bupalus piniorus* caterpillars, while birds had selected the less cryptic of a pair (Boer, 1971, in Edmunds, 1974).

A determination of whether the algal mask of *N. ursus* has a general advantage for the survival of these crabs can certainly be investigated satisfactorily in the field. However, although initially evolved to

meet a particular selection pressure, in reality, characters are often subjected to more than one selective force in nature. A separation of the multiple factors operating in the field, would be a difficult task, especially with nocturnally active, marine animals, such as *N. ursus*, and the predator used. For example, it would be extremely difficult in the field to ensure that both masked and unmasked crabs are equally exposed to the predator in all respects. Furthermore, the heterogeneity of the environment would make a determination of, for example, the effect of the background on crypsis extremely difficult. Consequently, in an effort to delineate the exact mode of operation of the algal mask, the experiments were conducted in the laboratory.

The major criticism levelled at laboratory studies is that the evidence can only be evaluated in the circumstances in which it was demonstrated. However, to a certain extent the same is also true of field studies as the selective forces to which an organism is exposed are not uniform throughout its range. Some degree of artificiality is always inherent in any laboratory situation, and the influence of such factors as the size of the aquarium and consequently the size and number of experimental animals used is unavoidable. However, such artificiality as exists must be balanced against the advantage of greater repeatability, better opportunities for observation and the ability to control, or at least account for, virtually every extraneous variable, as well as the variables under investigation.

Since it operates regardless of the presence of a predator, crypsis is categorised as a primary defence (Edmunds, 1974). The predator may not detect the prey at all (eucrypsis) or it may detect it but fail to recognise it as prey (special protective resemblance). When the primary defences fail, many animals can bring in secondary lines of defence (e.g., withdrawal, flight, deimatic behaviour, deflection of an attack or retaliation), which operate during an encounter with a predator. It is possible that the mask functions as one, or several, of these secondary defences instead of, or in conjunction with, being a primary defence. Once *N. ursus* is attacked, it is possible that toxic or noxious properties of the mask may discourage or prevent the ingestion of the crab. For example, certain hermit crabs (*Dardanus* spp.) are protected from octopuses by the commensal sea anemones (*Calliactis* spp.) (Ross, 1971; McLean & Mariscal, 1973). If the mask does have

unpleasant qualities, it is also remotely possible that the mask may be aposematic, warning potential predators of its noxious or toxic properties. Hence, a further aim of the research presented here was to determine whether the mask had a primary and/or secondary role in defence and its actual mode of operation. Consequently, to discover the defensive system of *N. ursus* it was first necessary to choose a suitable predator and then to consider the interaction(s) between *N. ursus* and this predator. From observations of the predatory interactions it was then possible to design experiments to delineate the exact mode of operation of the mask.

Cott (1940) and Breder (1946) argued that for predatory studies it is important to know the activity cycle of the prey, its behaviours, both when at rest and when disturbed, its relative conspicuousness throughout the normal range of its habitat and its potential and actual enemies. With the exception of actual enemies, this information was ascertained in Section I and suggests that a natural predator of *N. ursus* will be nocturnal (Remmert, 1969), with a bathymetric range from the intertidal area down to 73 m. This predator will require either acute visual discrimination under low light intensity, or rely on its chemo-tactile sense when hunting. For this predator, it will be important to know the times at which it feeds, its method of finding and capturing prey, the part played in hunting by the various senses, its powers of discrimination and memory, and the amount and nature of the food eaten compared with that which is available (Cott, 1940). There are very few species, whether hunter or hunted, for which adequate information on these points is available. Consequently, it was necessary to choose a predator for whom the majority of questions were already, or could be easily, answered.

In the following study of the interaction between *N. ursus* and the chosen predator, it was possible to determine the stages of this interaction that were affected by the mask and/or other behaviours exhibited by *N. ursus*. In addition, the effect of the mask on the crabs' survival was experimentally demonstrated and its mode of action was determined.

SECTION II

CHAPTER 12

THE PREDATORS: *OCTOPUS MAORUM* AND *ROBSONELLA AUSTRALIS*

12.1 INTRODUCTION

Octopuses are the only potential predators of *Notomithrax ursus* (Chapter 9) which are nocturnal, have the same habitat and bathymetric range (Nixon & Dilly, 1977) and whose general biology and predatory behaviour has been well studied (e.g., Wells, 1978). They use their visual, tactile and chemical senses when hunting and therefore afford a wider scope for testing the effect of the mask.

Two New Zealand species were used: *Octopus maorum* and *Robsonella australis*. These species were the most readily available and were recorded from the same localities as *N. ursus*. *O. maorum* is a natural predator of *Leptomithrax* (Hand, 1975), a genus closely related to *Notomithrax*. Brough (1965) reported that in the laboratory, *R. australis* attacked two large 'camouflaged' crabs (species not given). As there is little available specific information about the biology of New Zealand octopuses, it was necessary to undertake a preliminary study of both the predatory behaviour of *O. maorum* and *R. australis* and the techniques of maintaining healthy individuals in the laboratory.

12.2 METHODS

Octopuses were obtained from 0 - 73 m in the seas around Kaikoura, and Banks and Otago Peninsulas. Information regarding the 26 specimens used is contained in Table 12.1. Octopus 1 was used in Section I to confirm that these animals would prey upon *N. ursus* under laboratory conditions. The bulk of the information on general biology and predatory behaviour was gained from octopuses 2 - 8 and 19 - 21 but, where relevant, supplementary information was also gathered from the other individuals. Octopuses 9 - 18 were used to provide information on the interaction between *N. ursus* and predatory octopuses (reported in Chapter 14) and

Table 12.1 Details of the octopuses used as predators.

No.	Species	No. of gill filaments	Hectocotylus type	Sex	Weight (g)	Locality caught	Depth (m)	*N. ursus* recorded	Trapping method
1	*Octopus maorum*	13	-	F	35	Oaro Platform, Kaikoura	0.2	✓	Hand-netted
2	*Octopus maorum*	13	-	F	?	Kaikoura Peninsula	36.0	✓	Commercial net
3	*Octopus maorum*	13	-	F	?	Kaikoura Peninsula	36.0	✓	Commercial net
4	*Octopus maorum*	13	-	F	250	Kaikoura Peninsula	55 - 73	✓	Commercial net
5	*Octopus maorum*	13	-	F	300	Kaikoura Peninsula	55.0		Hand-netted
6	*Octopus maorum*	13	-	F	425	Banks Peninsula	?	×	Commercial net
7	*Octopus maorum*	13	Elongate	M	500	Banks Peninsula	?	×	Commercial net
8	*Octopus maorum*	13	Elongate	M	375	Kaikoura Peninsula	0.2	✓	Hand-netted
9	*Robsonella australis*	7	Club	M	35	Otago Peninsula	30.0	✓	Commercial net
10	*Robsonella australis*	6	-	F	50	Otago Peninsula	30.0	✓	Commercial net
11	*Octopus maorum*	13	Elongate	M	825	Kaikoura Peninsula	0.33	✓	Hand-netted
12	*Octopus maorum*	13	-	F	500	Kaikoura Peninsula	36 - 73	✓	Commercial net
13	*Octopus maorum*	14	-	F	650	Otago Peninsula	30.0	✓	Commercial net
14	*Octopus maorum*	13	-	F	375	Kaikoura Peninsula	0.33	✓	Hand-netted
15	*Octopus maorum*	13	-	F	375	Kaikoura Peninsula	55.0	✓	Commercial net
16	*Octopus maorum*	13	Elongate	M	700	Oaro Platform, Kaikoura	10.0	✓	Crayfish pot
17	*Octopus maorum*	13	Elongate	M	700	Kaikoura Peninsula	55.0	✓	Commercial net
18	*Octopus maorum*	13	Elongate	M	600	Kaikoura Peninsula	0.33	✓	Hand-netted
19	*Octopus maorum*	14	Elongate	M	300	Kaikoura Peninsula	55 - 73	✓	Commercial net
20	*Octopus maorum*	14	-	F	100	Kaikoura Peninsula	55 - 73	✓	Commercial net
21	*Octopus maorum*	14	Elongate	M	350	Kaikoura Peninsula	55 - 73	✓	Commercial net
22	*Octopus maorum*	13	Elongate	M	650	Kaikoura Peninsula	36	✓	Commercial net
23	*Octopus maorum*	13	-	F	500	Kaikoura Peninsula	55 - 73	✓	Commercial net
24	*Octopus maorum*	14	-	F	400	Kaikoura Peninsula	55 - 73	✓	Commercial net
25	*Octopus maorum*	13	-	F	300	Kaikoura Peninsula	55 - 73	✓	Commercial net
26	*Octopus maorum*	14	Elongate	M	650	Kaikoura Peninsula	0.33	✓	Hand-netted

octopuses 22 - 26 were used as the predators to determine if the mask was visually eucryptic (reported in Chapter 15).

12.3 RESULTS

12.3.1 Intertidal Abundance

Both *O. maorum* and *R. australis* were abundant in the intertidal zone only during the summer months (October - March).

12.3.2 Acclimation and General Behaviour

(a) Living area

To maintain a healthy octopus in the laboratory a surface area greater than the circle made by the outstretched arms of the octopus was required (Fig. 12.1). To enable the octopus to swim, the water has to be at least twice as deep as the depth of the octopus in the upright and alert position (Fig. 12.2).

(b) Home

When introduced into a novel area, octopuses immediately sought cover, preferably a hole or crevice, and if these were unavailable they would select a corner or shaded area. Confined spaces were preferred over large spaces. Thigmotaxis was more important than darkness in selecting a home or resting place; octopuses often wedged themselves between the clear viewing glass of the tank and the transparent perspex of the tray. Homes, comprising three bricks, one laid flat across a gap between two others, were readily accepted. *O. maorum* and *R. australis* regularly returned to this home using it as a place of rest, to digest prey and as a refuge from which to survey the area.

Within three days, sometimes as soon as a few hours, healthy undisturbed octopuses would venture out and 'explore' (see next section) their new surroundings. Those who did not, generally remained in their homes and refused to eat, eventually dying.

(c) Reaction to novelty

Novel objects were initially treated with caution and/or defensive reactions (see later) but later were gradually explored until finally the

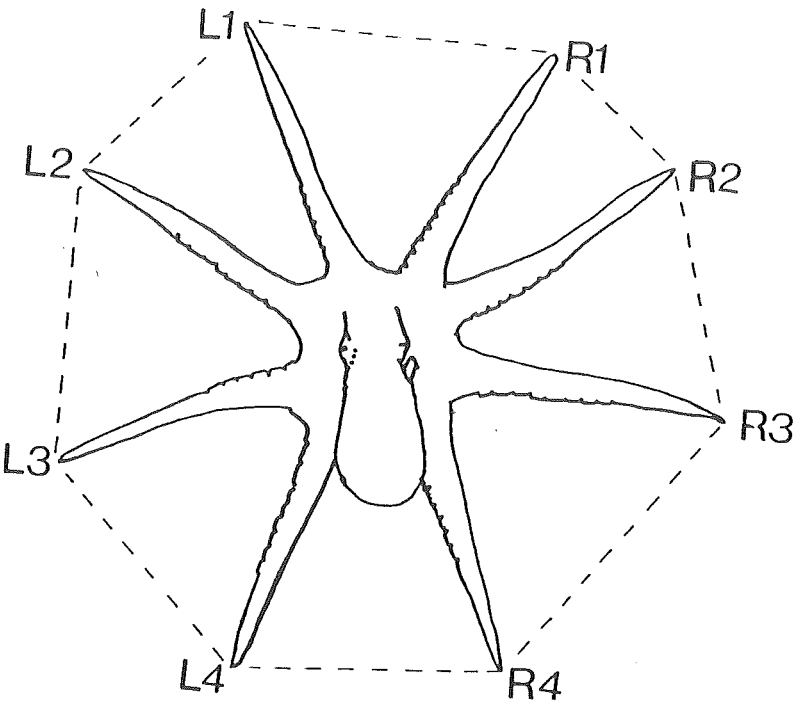


Fig. 12.1 Numbering of octopus tentacles. Broken line represents minimum area required for living space.

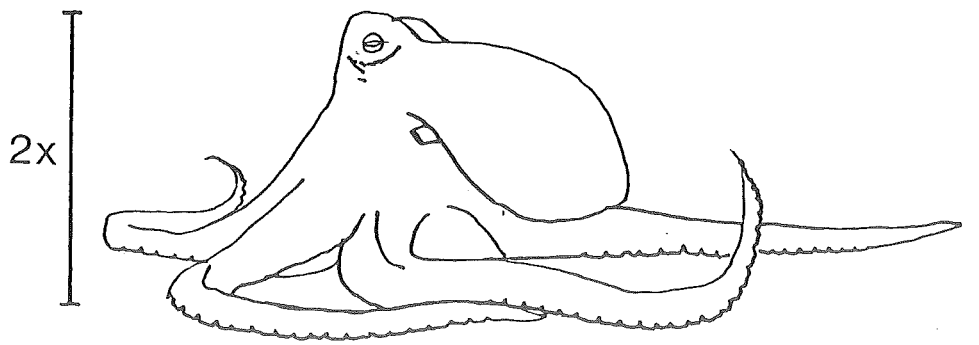


Fig. 12.2 Minimum depth of water required by octopus is twice body height in the alert position.

octopuses either ignored or used them. Exploration was expressed by two distinct behaviours.

Alert behaviour

When a novel stimulus was at a distance, the octopus sat at the entrance to its home, or other easily protected position, with its body hidden in the home and the tentacles outside but tucked back under themselves (see Fig. 12.14a). The eyes were open and the animal turned its head slowly back and forth, scanning the surroundings.

Tentacle probe

After a visual scan of the novel stimulus the animal would move towards the area, generally by a crawling action, and the arms, especially the tips, were systematically panned over the area/object; the suckers momentarily sticking to the surface. Holes and crevices were investigated by inserting as much of the arm(s) as possible.

(d) Movement

O. maorum and *R. australis* displayed two forms of movement.

Crawling

Crawling along the bottom was brought about by extending the front arms in the desired direction, clamping down the distal suckers, and then contracting the arms so that the body and hind arms were brought forward. Water ejected from the siphon aided sidelong or backward movement. These octopuses would also crawl on the distal parts of the arms rather like 'walking on tip-toe'.

Swimming

Swimming was achieved by powerful ejection of water from the siphon, i.e., jet-propulsion with the apex of the mantle in advance and the arms trailing out behind.

(e) Feeding

Both octopus species accepted live *Helice crassa, Hemigrapsus crenulatus, H. edwardsii,* masked and unmasked *N. ursus, N. minor, N. peroni, Petrolisthes elongatus* and *Pinnotheres novaezelandiae.* Octopuses remained

healthy and active on a ration of six crabs/day - larger crabs being used for larger octopuses.

(f) Responses to stimulation

(i) Aggressive behaviour. The sudden appearance and/or movements towards the octopus of relatively small, proximal objects elicited aggressive behaviour: the animal would lash out with its arms in the direction of the stimulus and attempt a tentacle attack (see later). This reaction was especially vigorous if the octopus was defending its home and/or eggs.

Aggressive display

With a larger and more distant stimulus, the octopus would glide towards it, the two foremost tentacles (R1, L1; Fig. 12.1) raised divergently and curled back towards the head (see Fig. 12.3). When within striking distance these two arms would make a tentacle attack.

Prolonged exposure to stimuli which normally elicited aggressive behaviour usually resulted in habituation to that stimulus, but if these stimuli were excessively aggressive the octopuses would display defensive behaviours.

(ii) Defensive behaviour

Defensive display

In contrast to distant or small stimuli, the sudden appearance and/or movement towards the octopuses of relatively large, proximal objects elicited a defensive display (Fig. 12.4). The animals flattened out, blanched and their eye rings darkened. This reaction could be followed by:

Flight. When in open water, octopuses took refuge by jet-propelled flight (see later), blanching as they went. If further molested, these animals emitted a puff of ink providing a dark screen between the stimulus and themselves and, where possible, sought cover.

If threatened, octopuses would generally flee straight into their homes, and in the absence of a home or if the threatening stimulus was between them and the home, they would often try to escape from the tank

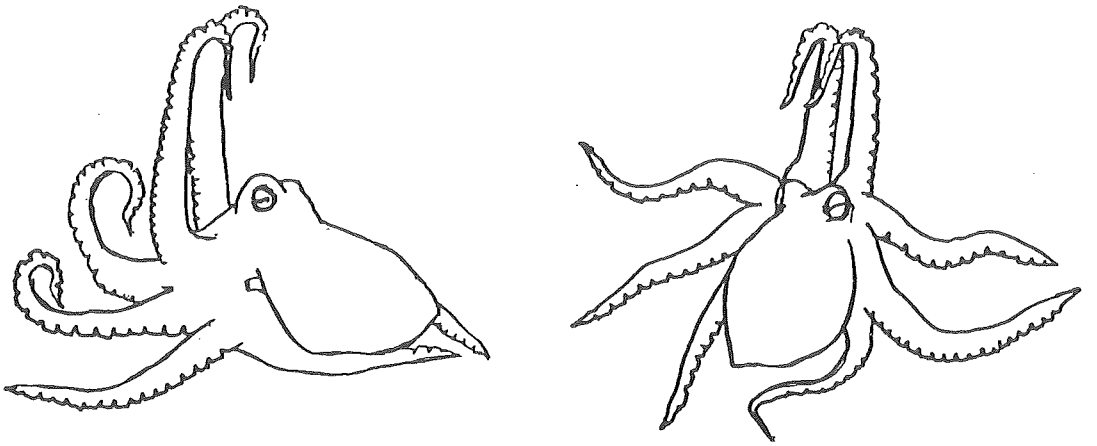


Fig. 12.3 Aggressive display of *Octopus maorum* and *Robsonella australis*.

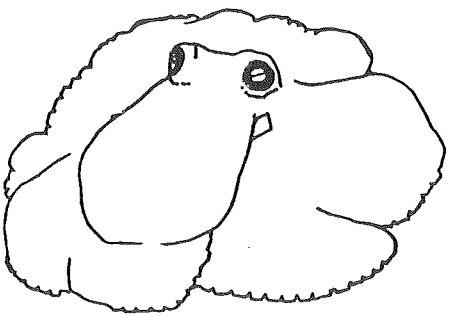


Fig. 12.4

Defensive (dymantic) display of *Octopus maorum* and *Robsonella australis*.

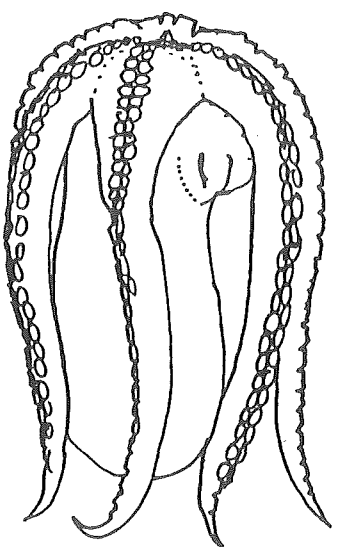


Fig. 12.5

Defence position (exposing oral region) of *Octopus maorum* and *Robsonella australis*.

completely. Otherwise, they would go into the 'defence' position (see below). Once ensconced in a home, octopuses would actively resist being evicted, especially if brooding eggs.

Defence position

When cornered, these animals would blanch and assume a posture with the beak and sucker-side of the back-curved arms presented uppermost (see Fig. 12.5). Excessively threatened octopuses would spend hours, and occasionally several days, in this defence position.

Water jetting

If further threatened, a cornered octopus would direct jets of water, expelled through its siphon, towards the threatening stimulus.

Although the expression of aggressive and defensive behaviours was uniform among the individuals observed, the strength of stimuli necessary to elicit these behaviours, and the length of time the responses were sustained, varied greatly between individuals.

(iii) Recovery from disturbance

Sulking

When sulking the octopuses remained inactive and hidden, refusing food even when it was placed in direct contact with the suckers. The length of this sulking period was proportional to the severity of the adversive stimulus.

Cautious behaviour

After adversive stimulation, octopuses would undergo a phase of cautious behaviour before resuming normal behaviour patterns. The form of cautious behaviour varied between octopuses and from trial to trial with the same octopus. During cautious behaviour the octopus would slowly approach the adversive stimulus, pause in front of it, then retreat and re-approach the stimulus several times before stretching out an arm(s) (usually the second or third) to momentarily touch the stimulus. This momentary touching of the stimulus could be either repeated or the octopus would retreat only to repeat the sequence, often approaching the stimulus

from a different angle. In addition, the octopus sometimes directed jets of water at the stimulus. Cautious behaviour was sometimes a partial parachute attack (see later): the octopus covered the crab with the outstretched web, then quickly withdrew before closing the web.

Retaliation by the prey often resulted in flight followed by sulking and/or bouts of cautious behaviour.

12.3.3 Predatory Behaviour

Observation of octopuses (4 - 18) with the crab species offered as food disclosed aspects of octopus predatory behaviour which were important to elucidating the function of masking behaviour.

(a) Propensity to hunt

(i) Uninterested behaviour. When not interested in its surroundings or in hunting, the octopus would sit, with its tentacles curled back under the web, generally resting (as evidenced by closed eyes and very slow ventilation) (Fig. 12.6). Prey could move over an uninterested individual without eliciting a response. An octopus could lose interest in a stimulus at any stage of the interaction, especially if the stimulus was weak, ceased, or was not recognised as a 'prey-associated' stimulus.

(ii) Appetitive behaviour. In general, octopuses showing either, or both, alert and tentacle probe behaviour would immediately hunt any potential prey they encountered. Such octopuses were termed 'appetitive'.

The readiness of the octopuses to hunt was affected by their activity rhythm. All captive octopuses exhibited a marked nocturnal activity rhythm, foraging from dusk until dawn. They were also opportunists, foraging during daylight if the opportunity arose.

When foraging at night, octopuses showed an adverse reaction to sudden light by freezing or gliding unobtrusively out of the light, abandoning their previous activity.

A preliminary experiment, using octopuses 4 and 5, showed that

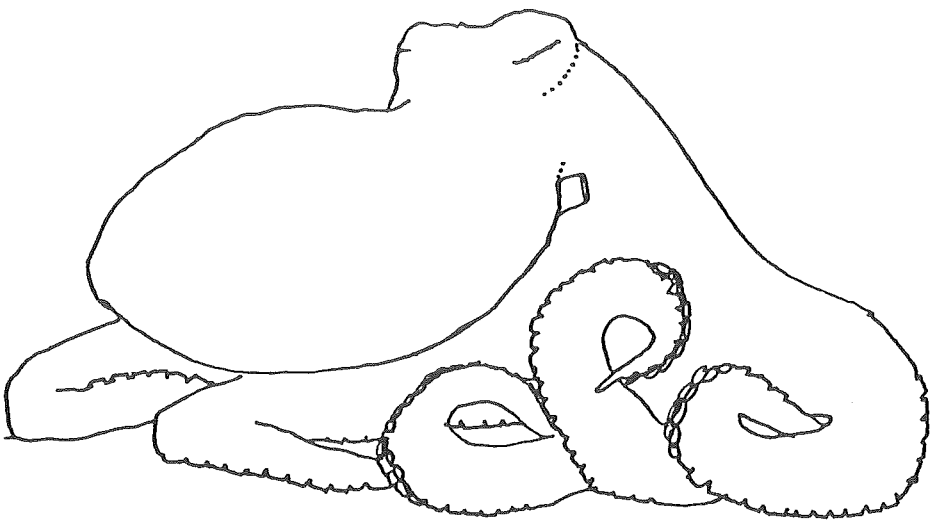


Fig. 12.6 The uninterested position shown by *Octopus maorum* and *Robsonella australis*.

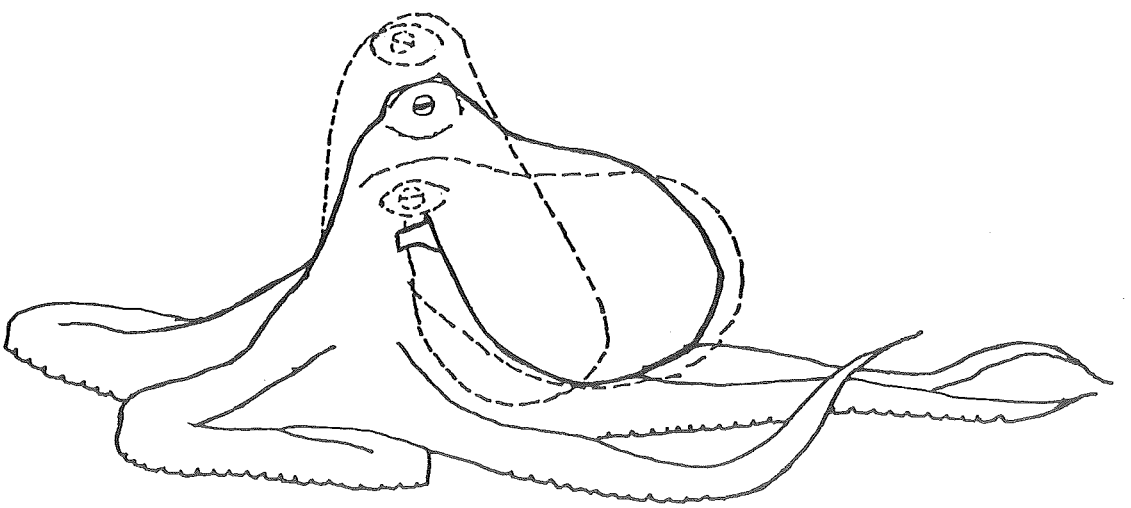


Fig. 12.7 Bobbing behaviour shown during attention to a visual stimulus shown by *Octopus maorum* and *Robsonella australis*.

when six to eight crabs were presented/trial against a contrasting background, which did not afford hiding places, increasing the length of food deprivation resulted in heavier predation (Table 12.2). Octopuses can store several prey at once by virtue of having eight sucker-clad arms and a web which can be formed into a holding purse (Fig. 12.14d). Both *O. maorum* and *R. australis* continued to hunt whilst holding several prey. Cessation of hunting was governed solely by a physical inability to hold additional crabs, and it was not unusual to observe an octopus catch one crab at the expense of losing two earlier victims. While ingesting crabs, octopuses usually would not hunt until all prey were consumed. All four *O. maorum* females who laid eggs whilst in the laboratory accepted food whilst brooding but they did not hunt prey which could not be reached with the tip of the most distal arm whilst the opposite arm was touching the eggs.

The propensity to hunt was adversely affected by the novelty of both the prey and the immediate environment, but by the third day in a new area the octopus would generally attack a crab within 3 - 4 seconds of detecting it. However, individuals differed widely not only in the delay and caution exhibited before attacking crabs but also in the propensity to attack or to hunt from day to day.

Finally, the propensity to hunt was adversely affected by disturbance from external stimuli, such as the experimenter, but this problem was overcome easily by the use of screens.

(b) Searching behaviour

Visual contrast of the stimulus against the background influenced whether the search is visual or tactile-chemical. Octopuses were most likely to exhibit alert behaviour if the prey were presented against a contrasting background. Conversely, the octopuses were more likely to exhibit tentacle probing if the prey were against a simulated natural background (*Corallina* sp. covered rocks and a large clump of *Halopteris spicigera*). With tentacle probing especially, searching increased if the octopus had previously been rewarded by capturing a crab in that area. The 'memory' of prior capture in that area could last approximately 14 days, and if the prey had actually been ingested, the 'memory' could last 15 days.

Table 12.2 Effect of food deprivation on subsequent predation of crabs by *Octopus maorum* in the laboratory.

Days Without Food	Total Number of Crabs Presented	Percentage of Crabs Eaten
0	44	34.1
1	18	44.4
3	8	75.0
7	6	100.0
14	6	83.3

Speculative pounces

If an octopus had previously captured prey in a particular area, it subsequently made speculative pounces on the area concerned. This behaviour involved parachute attacking (see later) the area, and then pausing whilst the area under the web was systematically tentacle probed.

(c) Stimulus perception

(i) Distal perception. Both *O. maorum* and *R. australis* were capable of visual and non-visual perception of stimuli at a distance. All octopuses tested could visually detect *N. ursus* (masked and unmasked), *Hemigrapsus edwardsii* and *Petrolisthes elongatus* crabs against contrasting (plain grey concrete, yellowish brown wood, or black polythene) and semi-natural backgrounds (algal covered rocks, Chapter 13). Under natural and fluorescent daylight (intensity 3.2 foot lamberts) these stimuli were perceived at least 2 m away and 0.78 m under monochromatic red light at intensities of 0.54 and 0.11 foot lamberts. Visual perception was demonstrated by the fact that stimuli elicited a response whether they were on the same or opposite side of the glass viewing panel. When this glass was screened with black polythene blinds, the octopuses no longer reacted to external stimuli. Visual perception was very keen; under the lowest red light intensity, even slight movement such as a segment of a crab's leg could elicit a response.

The non-visual perception of distal stimuli was demonstrated by the fact that both the movement of crabs behind a black screen, or in dense algal growth, and tapping the wooden side of the experimental tank elicited a response from both octopus species.

The perception of distal stimuli was shown by one of two reactions: immediate attack or 'attention' (see below) behaviour. The occurrence of either behaviour was governed by the type of stimulus received, its strength, and the prior experience of the receiver.

'Attention'

During 'attention' the octopus would pause (if previously moving), raise its head which was then inclined towards or turned sideways to the stimulus so that one eye directly faced the stimulus. Next, the head was

'bobbed' by being repeatedly raised and lowered (Fig. 12.7). During 'attention' the octopus typically darkened in colour.

'Excitation'

Attention was often followed by an 'excitation' bout, where the octopus writhed the tentacles close to and over the body, rapidly coiling and uncoiling them and rubbing the suckers together. This arm writhing was accompanied by a rapid pumping action of the mantle cavity (resulting in blowing jets of water?) and a rippling of the web (see Fig. 12.8).

'Pacing'

Excitation was often accompanied and/or followed by 'pacing'. This involved roving back and forth along the immediate area as if to further scrutinise the stimulus.

Both attention and pacing behaviours appeared correlated with prey discrimination as they were exhibited when the stimulus was (for humans at least) difficult to detect or when the stimulus immediately disappeared either physically or perceptually.

(ii) Proximal perception. Uncertainty about a perceived stimulus, or accidental contact with a stimulus, resulted in the octopus seeking contact with that stimulus.

Sucker exploration

This was similar to the tentacle probe method, but instead an individual stimulus object was systematically investigated by the suckers which, although making contact, did not grasp nor immobilise the object (Fig. 12.9). In effect, the octopus was utilising an object-concentrated search.

The sensory capacities of the suckers were not investigated, although the octopus could differentiate between animate and inanimate objects. Inanimate objects such as brushes, air hoses, and nets were held only briefly (< 20 seconds) and if pulled away were released within five seconds. Conversely, animate objects were often held for many minutes and if pulled away were grasped tighter, the octopus often using

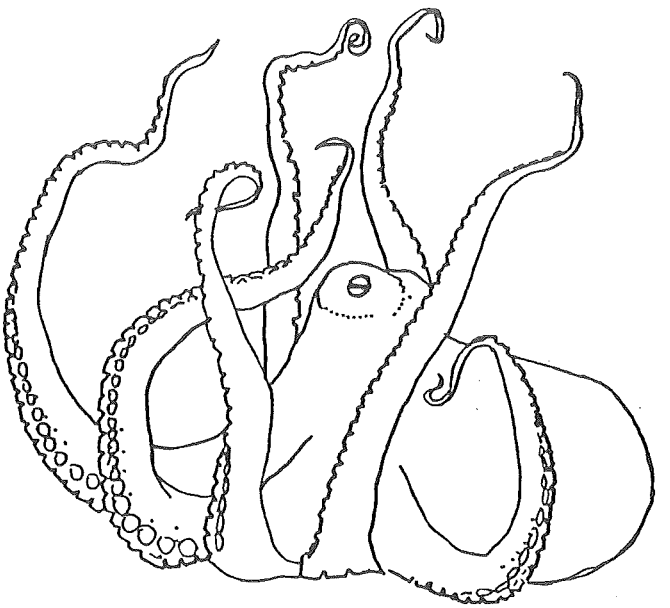


Fig. 12.8 Excitation behaviour of *Octopus maorum* and *Robsonella australis*.

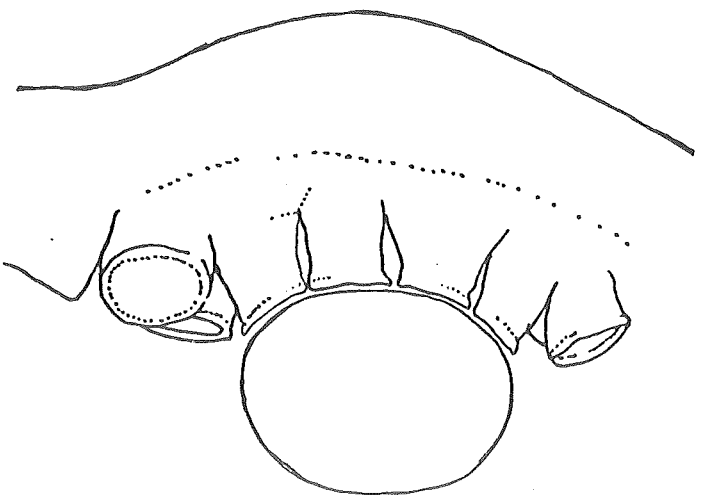


Fig. 12.9 Detailed view of octopus Sucker Exploration of an object.

additional arms. Sucker exploration could result in uninterested behaviour or a tentacle attack (see later) depending on the information received.

(d) Prey discrimination

Factors affecting prey discrimination were investigated by a preliminary experiment in which 20 masked and 20 unmasked *N. ursus* were presented against a contrasting background (plain yellowish brown wood) under dim red light (intensity = 0.54 foot lamberts) to octopuses 6 and 7. On some trials, the observer's view of the variable(s) under consideration was obscured by the movement of either the octopus or crab. Consequently, these trials were abandoned and not all the following analyses concerned all 40 trials.

(i) Prior contact with the prey. There was no significant difference ($\chi^2 = 2.291$, $p > 0.05$) between crabs attacked, by either tentacle or parachute methods (see below), subsequent to contact with the octopus, and those crabs which were parachute-attacked without prior contact with the octopus (Table 12.3). Hence, the octopuses were capable of remote detection of the crab prey.

Table 12.3 The effect of prior contact with *Notomithrax ursus* on the subsequent attack of that prey by *Octopus maorum*.

	Prior Contact	No Prior Contact	Total
Attacked	14	18	32
Not attacked	0	4	4
TOTAL	14	22	36

(ii) Prey movement. Movement was a very important cue in eliciting attacks by the octopuses: significantly more moving than immobile crabs were attacked ($\chi^2 = 4.538$, $p < 0.05$) (Table 12.4).

Table 12.4 The effect of prey movement on subsequent attack of *Notomithrax ursus* by *Octopus maorum*.

	Moving	Immobile	Total
Attacked	23	7	30
Not attacked	1	3	4
TOTAL	24	10	34

Contact with the prey did not affect the importance of movement of eliciting attacks (χ^2 = 0.4574, n.s.) (Table 12.5).

Table 12.5 The effect of prior contact with a prey on the subsequent attack of that moving prey by *Octopus maorum*.

	Moving Crabs		Total
	Contact	Not Contact	
Attacked	7	16	23
Not attacked	0	1	1
TOTAL	7	17	24

(iii) Body outline of prey. The effect of body outline (shape) against a contrasting background was investigated by considering the effect of the algal mask on attacks by octopuses. The algal mask did not affect the number of attacks on *N. ursus* (χ^2 = 0.2286, n.s.) (Table 12.6) nor did it affect the order in which the crabs were attacked. (Us = 166, n.s.) The importance of movement in eliciting attacks by the octopuses was also not affected by the algal mask (χ^2 = 0.8829, n.s.) (Table 12.7).

Table 12.6 The effect of the algal mask on attacks of *Notomithrax ursus* by *Octopus maorum*.

	Masked	Unmasked	Total
Attacked	18	17	35
Not attacked	2	3	5
TOTAL	20	20	40

Table 12.7 The effect of the algal mask on the subsequent attack of moving *Notomithrax ursus* by *Octopus maorum*.

	Moving crabs		
	Masked	Unmasked	Total
Attacked	11	12	23
Not attacked	0	1	1
TOTAL	11	13	24

(iv) Size of prey. The size of the crabs did not appear to influence the effect of movement, contact, nor the presence of the algal mask in eliciting an attack by the octopuses. The two octopuses exhibited no difficulty in handling or restraining crabs of CL 19.9 - 35.10 mm and attacked prey ranging in size from as small as 12 mm CL to prey approximately as large as their own mantles. Larger stimuli elicited defence or flight behaviour.

(v) Learning. The prior experience of octopuses had a marked effect on their reaction. When first isolated in a tank, an octopus may attack unfamiliar or novel objects/crabs after a long delay. However, with successive presentations of the stimulus the probability of an attack increased, while the time to attack decreased. This 'learning' resulted

in appetitive octopuses attacking, within two seconds, 99% of crabs presented. *O. maorum*, at least, was capable of learning certain tasks with only one trial. For example, in the process of exploring the new tray (Chapter 14) octopuses 4, 15 and 17 discovered that they could slip down the space between the side of the tray and the side of the tank. From then on these octopuses would immediately go to this gap without having to find it by exploring the tray with their tentacles.

(vi) Memory. Retention of learned behaviour by *O. maorum* and *R. australis* was demonstrated by the fact that once they had learned to attack an object they responded the same way, and just as quickly, when next exposed to the same stimulus. Existence of memory was also shown by their area-concentrated-searching behaviour, several days after having been previously reinforced in that area.

(e) Prey selection

The octopuses tended to select prey types previously captured, especially if these prey were particularly conspicuous against a background or showing unusual behaviour (e.g., crabs which had been turned upside down, and were struggling to right themselves, were quickly attacked). Selection of prey was also influenced by that prey's secondary behaviour. For example, large crabs, which retaliated by pinching the octopus, were hastily released and often not attacked again (Table 12.2). Subsequent immobility of a prey, especially if detected from a distance, often resulted in that prey being ignored (Chapter 14).

(f) Hunting method

Both *O. maorum* and *R. australis* employed a variety of methods of hunting crabs: ambush, stalking, a jet-propelled rush, and digging.

Ambush

This was the only passive hunting method: the octopus sat immobile, in the alert position, at the entrance to its home or some other vantage point. When the prey was within striking range, the octopus would lash out and make a rapid tentacle attack (see below). Ambush could be

accompanied by distinct changes in colour and texture. When amongst clumps of *Halopteris spicigera*, both *O. maorum* and *R. australis* would flush darker and develop irregular papillae over the body, web, and upper tentacles (Fig. 12.10). These papillae were most pronounced on the mantle area. Octopus 16 was also observed to erect these papillae on one occasion when it was not amongst the weed but was observing an unmasked crab moving its chelipeds amongst the weed.

Stalking

Several variations of stalking prey were observed, but all involved a slow, stealthy approach. Generally, the prey was approached indirectly, the octopus circling round, often advancing from the rear. One of two characteristic postures were maintained during this approach. Most commonly, the head was held high and the arms were curled compactly underneath, and when within striking distance the prey was parachute-attacked. When crabs were presented against the semi-natural background, octopus 15 was observed to lie on its side and, keeping close to the substrate, slowly glided along until it was underneath the crab when it would make a tentacle attack, slowly unwinding a tentacle towards the prey.

Stalking often involved elements of cautious behaviour and may have resulted from uncertainty by an octopus about a particular prey. Stalking could also be accompanied by distinct changes in colour and texture. During stalking the colour change appeared to be a form of countershading with the octopus flushing darker on one side of its body and paling on the other. The contrast between light and dark sides was a distinct straight line dividing the body between the eyes. The side nearest the prey darkened and if the octopus turned round it flushed accordingly (Fig. 12.11).

Jet-propelled rush

The most common pattern of hunting was a visually directed jet-propelled rush at the prey culminating in a parachute attack. On sighting a distant stimulus the octopus would flush darker and then slide out of its home (or off its vantage point) and swim smoothly and rapidly towards the prey, L1 and R1 arms outstretched. Occasionally, the approach was backwards, the arms trailing until the moment of seizure. As the prey was reached the octopus would make a parachute attack (see Fig. 12.14b).

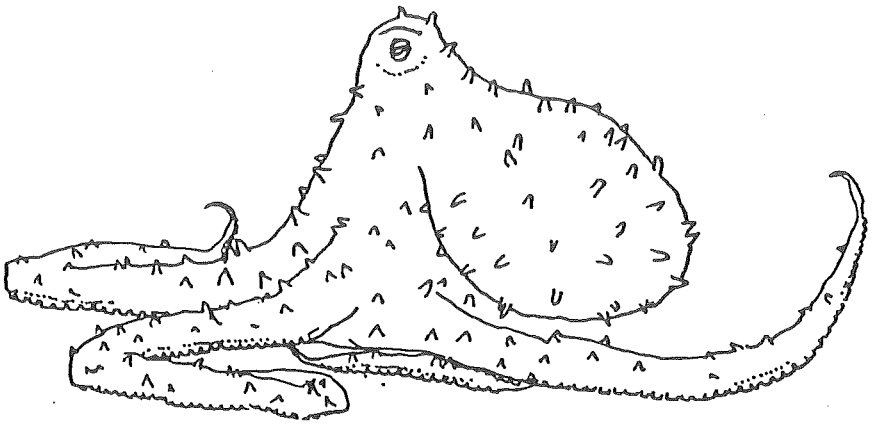


Fig. 12.10 Erection of body and tentacle papillae by *Octopus maorum* and *Robsonella australis* during hunting in algae.

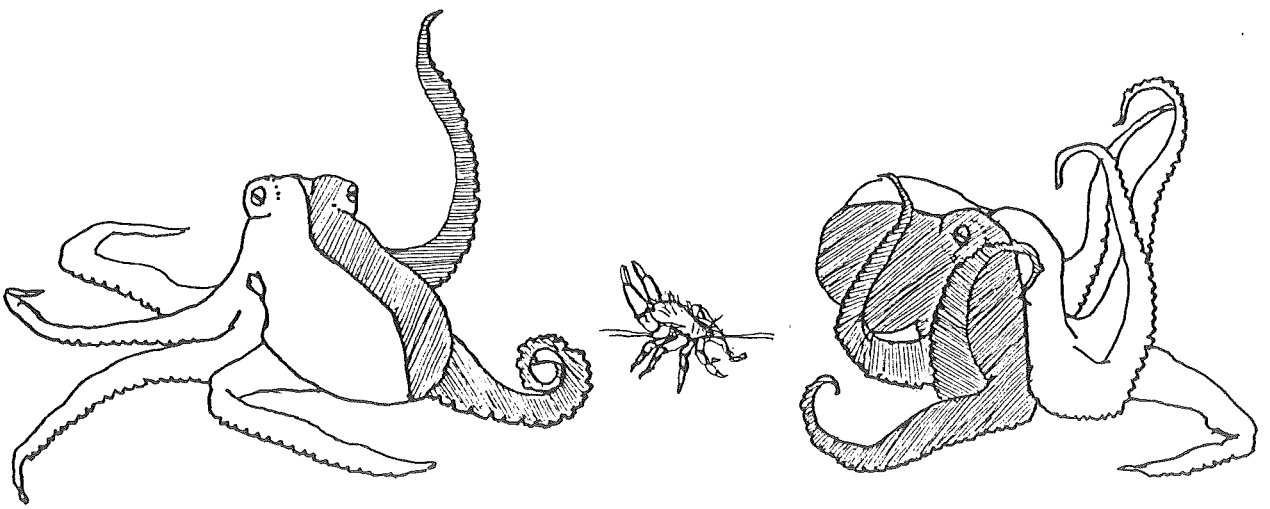


Fig. 12.11 Darkening of body colouration of *Octopus maorum* and *Robsonella australis* in relation to the position of a crab.

Digging

Both *O. maorum* and *R. australis* were very persistent hunters. If a pursued prey escaped by hiding amongst the algae or in rock crevices, octopuses would systematically dig for them. Material removed from the hole was gathered under the web which was pursed at the bottom to form a bag, and the octopus would walk, on the free portions of its arms, to the area just outside the entrance to its home and dump its load. A subsequent blast of water from the funnel was very effective in blowing away the finer particles. Periodically the octopus would cease digging, probe the crevice surrounding the hole it had made and then would often change the direction of excavation. This digging behaviour would continue until the prey was caught or there was no further material to be removed.

Both octopus species were also very adept at prising prey out of small spaces by placing a tentacle on either side of the prey, compressing the tentacles so that the prey was, in effect, 'popped' out (see Fig. 12.12).

(g) Attacking behaviour

Octopuses had two forms of attacking their prey: tentacle and parachute attacks.

'Tentacle attack'

During this form of attack the octopus would throw out a tentacle which was unwound towards the prey. When contacted the prey was wrapped around by the tentacle (see Fig. 12.13).

'Parachute'

As the octopus neared the prey it spread its tentacles and alighted upon the prey from above, enveloping it in the web (see Fig. 12.14c).

Attacking behaviour was influenced by the animal's prior learning. Familiar prey, especially if other specimens had actually been eaten, were generally 'parachute' attacked rapidly without any signs of cautious behaviour. Tentacle attacks were employed with novel, retaliatory, or very close prey. At the moment of attack the octopuses were commonly pale, flushing as they carried the prey home. Mode of attack was also affected by prey size: smaller prey were parachuted.

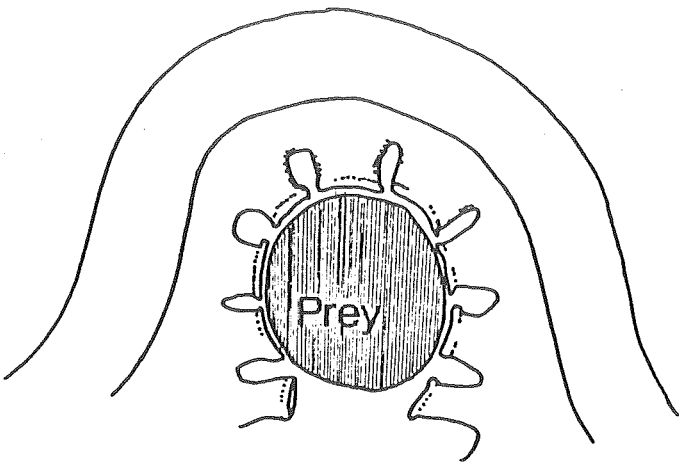


Fig. 12.12 Detailed view of *Octopus maorum* sucker action during digging behaviour.

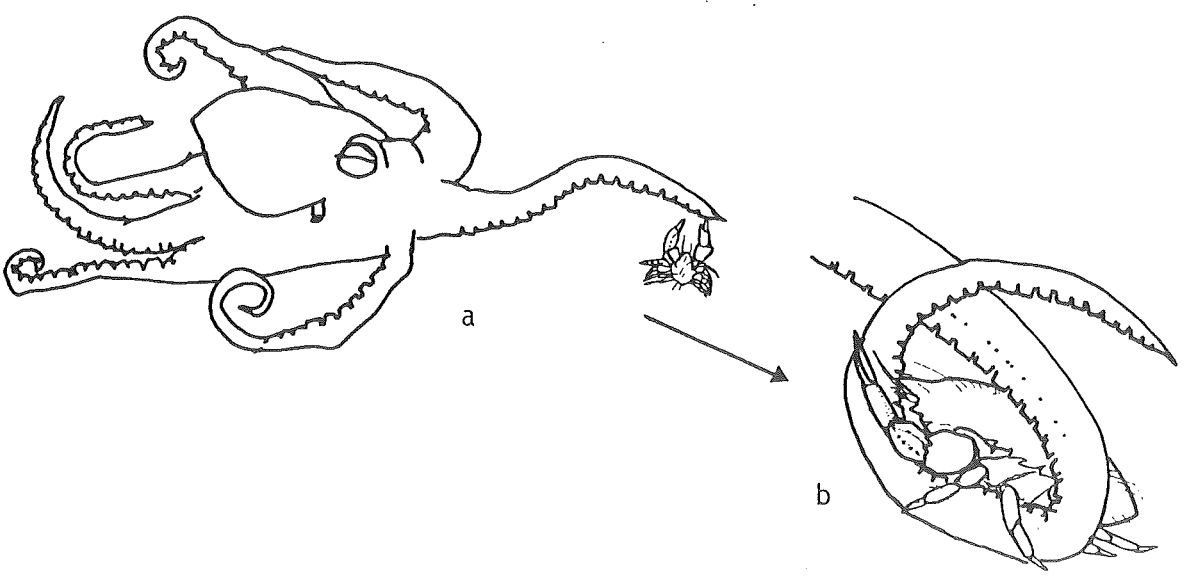


Fig. 12.13 Tentacle Attack showing octopus approaching crab (a) and capturing prey (b).

(h) Prey retention

Prey were retained by clamping the suckers on to the prey's exoskeleton. Only one octopus, number 13, was unable to retain and/or transport crabs, especially *N. ursus*, both masked and unmasked. In this case, the suckers did not appear to be able to clamp on to the crabs. As this inability only occurred in the experimental, but not home, areas of the aquarium, it was probably an experimental artefact.

(i) Prey transport

The decision to accept/reject the object held could be made merely by a surface examination of the object by the suckers, without passing it under the web. Captured objects were transported by being transferred from one sucker to another as the tentacle was curled over and over. If the prey was rejected, the curling action proceeded in the direction of the tentacle tip and the prey was flicked away. Conversely, if the prey was accepted the arm encircling the prey was curled towards the web.

(j) Feeding position

Once under the web the prey were again subject to an accept-reject decision. If rejected, the suckers released their hold and the prey was allowed to fall. If the prey was accepted, the interbranchial web was pulled together to form a watertight purse (see Fig. 12.14d). At this stage the octopus could either store the prey and become ready to hunt again or it could commence eating its prey.

(k) Prey immobilisation

Even in the 'purse' the prey would continue to struggle and then suddenly all movement ceased. If removed or dropped at this stage, the prey were either totally immobile or their movements were very sluggish and erratic, suggesting that they had been incapacitated. As they bore no signs of physical damage they were probably immobilised by chemical means. Crabs could be immobilised within 1.5 min of the web being pursed and would stay cataleptic for up to four hours.

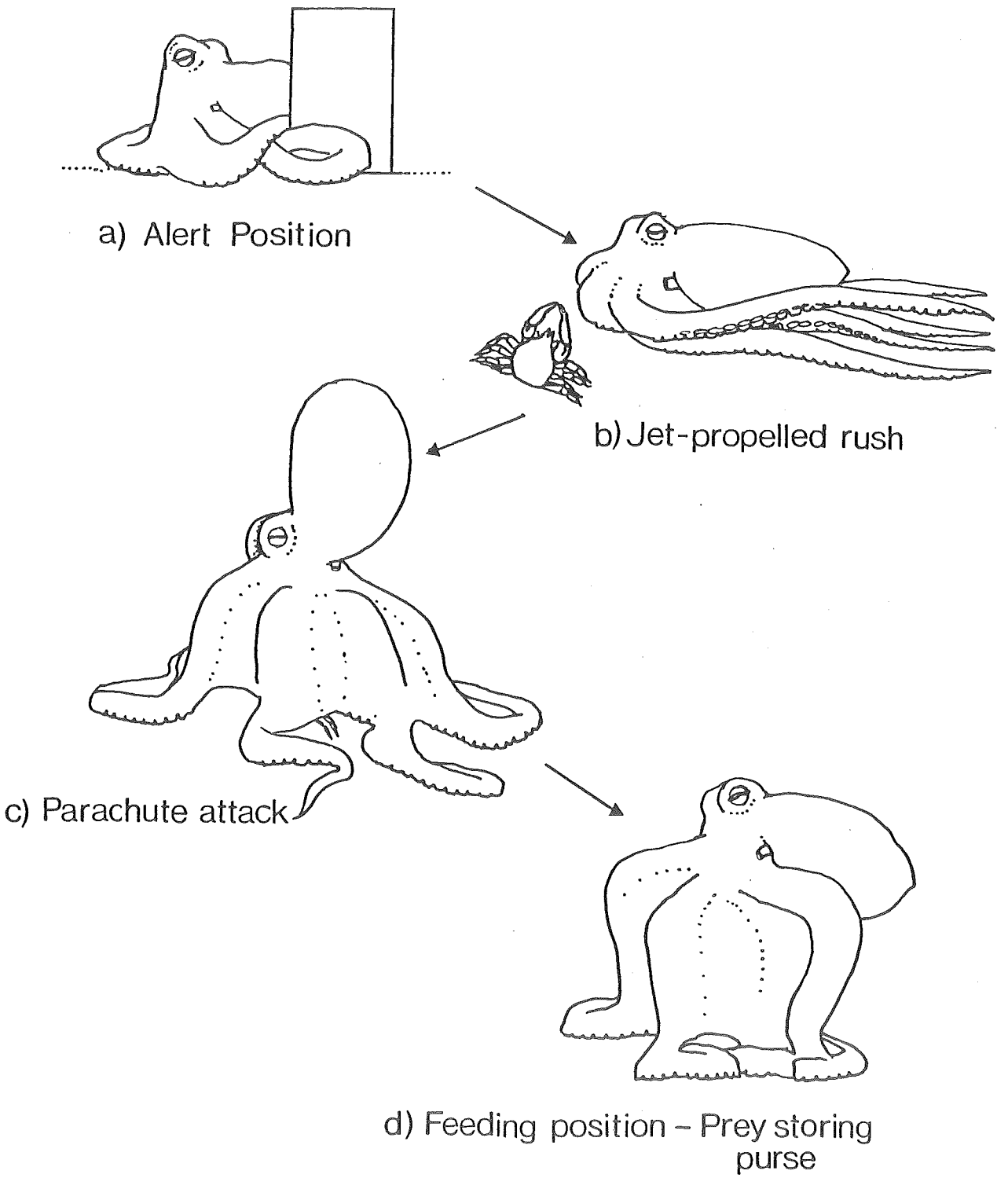


Fig. 12.14 Complete octopus attack sequence from perception of prey to feeding.

(1) Ingestion of prey

After the octopus had subdued the crab it proceeded to split open the carapace starting at the rear of the carapace. The internal structures were then removed. When all the meat had been extracted, the purse was opened out and the empty exoskeleton was released.

12.4 DISCUSSION

Cott (1940) outlined the important facts to be determined for the predator. This study has established, for *O. maorum* and *R. australis*, the feeding times, method of finding and capturing prey, and the part played in hunting by the various senses. Although the amount and nature of the food consumed was determined in the laboratory, a comparison with the field was not attempted.

12.4.1 Comparison with Other Cephalopods

The majority of behaviours exhibited by *R. australis*, and especially *O. maorum*, are the same as those shown by other cephalopods, particularly *O. vulgaris*, but also *O. appollyon*, *O. cyanea*, *O. joubini*, *O. rubescens*, *O. rugosus*, *O. tetricus*, and *Eledone moschata* (Cowdry, 1911; Taki, 1941; Boycott, 1954; Sutherland, 1958; Lane, 1960; Wells, 1962, 1978; Rhodes, 1963; Wood, 1963; Dilly *et al.*, 1964; Maldonado, 1964; Woods, 1965; Altman, 1967; Russell-Hunter, 1968; Packard & Sanders, 1969; Taylor & Chen, 1969; Yarnall, 1969; Wells & Wells, 1970; Thomas & Opresko, 1973; Kayes, 1974; Neil & Cullen, 1974; Moynihan, 1975; Joll, 1976). However, there were some differences and these will now be discussed.

The aggressive behaviour displayed by *O. maorum* when confronted by a larger and more distant stimulus is also observed in *O. vulgaris* and is termed a 'flamboyant' posture (Packard & Sanders, 1969). Moynihan (1975) maintained that this behaviour was never performed by adults, that the arm movements were combined with several colour arrangements (which are thought to be cryptic in the octopus) and this posture was primarily an anti-predator adaptation indicating 'alarm'. Only one adult *O. maorum* (No. 26, a male) displayed this behaviour. No major colour changes, during this behaviour, were observed in any of the octopuses, although slight changes may have gone unnoticed under the red light which altered

my perception of their true colours. In *O. maorum* this behaviour was not fully one of alarm, as it was always completed by a tentacle attack on the stimulus object. However, the raised divergent arms may have been the result of internal ambivalence concerning the fight or flight decision.

Generally, brooding female octopuses have been reported to refuse food and to die soon after the eggs hatch (Lane, 1960; Joll, 1976; Wells, 1978). However, Thomas & Opresko (1973) reported that although *O. joubini* females would not leave their eggs to feed, they would generally attack and consume a crab that wandered into their den. These workers also found that the females did not always die after the eggs hatched and they attributed this to the availability of food during brooding. *O. maorum* were not only observed to feed while brooding, but also to leave their eggs and go for short sorties around their tanks capturing any crabs encountered. The differences between *O. maorum* and other species may be due to two factors - one an experimental artefact, the other a species difference. In both the experimental and home cages the prey were only just out of tentacle reach when the octopuses were tending eggs. *O. maorum* lays eggs on an open surface and sits over them. *O. vulgaris*, however, lays eggs in holes, erecting massive stone walls at the entrance (Woods, 1965).

12.4.2 Appetitiveness

Preliminary work with *O. maorum* and *R. australis* demonstrated that various other factors had a great influence on their propensity to hunt. Their activity rhythm, prior experience with the stimulus, state of physiological and sensory disturbance, brooding, and prey storing were all involved. A further complicating factor was that individual octopuses differed in the amount they were affected by all these factors, between different animals, and the same octopus at differing times.

The problems of controlling all factors affecting the feeding behaviour of the octopuses, especially prior experience, were almost insurmountable. Since this thesis was only concerned with octopuses which were ready to hunt and not why they were hunting, it was decided not to try to control and match all the affecting variables, but to expose the octopuses to trials when they were showing 'appetitive'

behaviour. As the trials were continued until the animals stopped exhibiting appetitive behaviour, they were performance-related not time-related.

12.4.3 Searching Technique

Predators can employ two types of searching method: area-concentrated and object-concentrated (Curio, 1976). The latter form is thought to involve the formation of a searching image, which Curio defines as a "perceptual change which leads to an improvement of searching performance as measured by items found". The existence of a predator searching image is particularly difficult to demonstrate (Krebs [1973] provides detailed discussion of this). In particular, it often seems difficult to separate out "learning to see" and preference for familiar food types. Consequently, there is considerable controversy over whether or not the phenomenon in fact exists. The existence of searching image was not investigated in *O. maorum* and *R. australis*. However, it is conceivable that they are capable of this form of searching as they were shown to possess four of the six criteria listed by Curio (1976) as characterising this phenomenon. These attributes were (1) rapid acquisition, (2) high retention, (3) rapid extinction, and (4) the reinstatement of a learned behaviour after just one instance of the stimulus occurring. An alternative theory to hunting by searching image is the profitability of hunting theory (Krebs *et al.*, 1977) but this was not investigated.

Area-concentrated searching for prey may be of two types: short-term, where the predators can make a rapid survey of a large area and unless something at once attracts their attention can continue on their way, or the predators can engage in a long-term area-concentrated search, moving slowly, making a minute search of areas with a much smaller radius. In the laboratory at least, octopuses engaged in long-term area-concentrated searches both distally and proximally for near and distant prey. This long-term searching was affected by their subsequent reward. If they made an attack the probability of further searching in that area increased, and further increased if the prey were actually ingested. Thomas (1977) found the same phenomenon in sticklebacks (*Gasterosteus aculeatus* L.) and he termed this behaviour 'area-restricted' search. Conversely, he observed 'area-avoided' search after a prey had been rejected. Following the rejection of an attacked prey by *O. maorum* and *R. australis* there was no

noticeable 'area-avoided' search, but this may have been a function of the small size of the hunting area. Yarnall (1969) reported the existence of an area-concentrated searching technique in *O. cyanea* which he termed 'speculative pouncing'. The same behaviour was also observed in *O. maorum* but only subsequent to having made an attack in that area.

The 'memory' controlling this feedback was effective for *ca.* 14 days if the prey had not been ingested and for *ca.* 15 days if the prey had been eaten. The existence of this 'memory' is in agreement with Boycott (1954) who found that *O. vulgaris* had a short-term memory of *ca.* 30 min and a long-term retention of two weeks or longer.

12.4.4 Perception

Predators have a chance to detect a given prey only when within a certain distance of this prey. This distance will depend on the properties of both the predator and the prey. De Ruiter (1956) maintained that a given prey may be said to be surrounded by a definite 'danger zone'. For both *O. maorum* and *R. australis*, prey presented in the laboratory against a contrasting and semi-natural background had a 'danger zone' of at least 0.78 m (i.e., the length of the experimental aquarium).

O. maorum and *R. australis* were both capable of non-visual as well as visual perception of stimuli, although they predominantly relied on their visual sense. Traditionally, they would be referred to as visually hunting predators. However, Robinson (1969) stressed that this term implies that vision is the only sensory modality which the animals used in hunting. He proposed the term 'visually oriented' as being a better description, and in the case of *O. maorum* and *R. australis* this would definitely be more accurate.

The perception of stimuli by *O. maorum* and *R. australis* was signalled by the exhibition of attention, excitation, and pacing behaviours. Wells (1978) attributed the 'bobbing' phase of the attention behaviour to a ranging by parallax which is a reasonable hypothesis in the light of Messenger's (1977a) finding that attacks by *O. vulgaris* are monocular. The arm coiling behaviour observed during excitation has not been mentioned for *O. vulgaris* in this context. However, Lane (1960) described this behaviour when *O. vulgaris* was sloughing off dead skin and sucker discs,

so in the present context it may well be a displacement activity. The arm coiling was accompanied by a rippling of the web. Wells (1978) described this rippling during the bobbing phase of attention behaviour and hypothesised that in *O. vulgaris*, at least, this rippling served to flush the potential prey out of cover. In both *O. maorum* and *R. australis* the arm writhing was also accompanied by a rapid pumping action of the mantle cavity. This resulted in jets of water being directed at the stimulus and may also serve to flush the prey out of cover.

Although movement was found to be a very important cue for *O. maorum* and *R. australis*, it was, however, not necessary to elicit an attack under certain circumstances. The rapid form of attack, by parachuting, was only elicited by non-moving prey if that prey had moved previously or if another prey had been successfully attacked and/or ingested in the immediate past. Otherwise, stationary crabs were only tentacle attacked (the more cautious approach) especially if they were accidentally contacted. There has been some controversy in the literature over the necessity for prey movement in eliciting attacks by octopuses. Earlier workers such as Cowdry (1911), Boycott & Young (1956), and even Lane (1960) held that movement was absolutely necessary to elicit attacks. Wodinsky (1971) held that movement was not necessary to elicit attacks. Wodinsky may be correct, but his reasoning and experiments are open to criticism. The assumption underlying all his supporting evidence is that all attacks are elicited by visual cues alone. However, the manipulation of objects, speculative pounces, lack of discrimination between live and sealed empty shells, and the observation that octopuses would reach out of the water to pull immobile gastropods off the rocks, as reported by Wodinsky, ALL involve tentacle attacks and hence the stimuli eliciting attacks could be chemo-sensory and not visual. Since octopuses will feed on gastropods and lamellibranchs which move very little may also be explained as the result of non-visual cues as these animals are, in all probability, tentacle attacked. Wodinsky then discusses the fact that many octopuses and their prey are nocturnal so they must use senses other than vision. However, this is not necessarily the case. Both starlight and moonlight penetrate the shallow coastal waters and, as my observations and experiments have demonstrated, *O. maorum* and *R. australis*, at least, have exceptionally acute vision under red light of low intensities.

O. maorum and *R. australis* attacked crabs and various other objects that varied from 3 mm long up to approximately the diameter of their own mantles. This finding is in agreement with Stein & Magnuson (1976) who concluded that "predators operate on a continuum: prey must be large enough to see but small enough to handle". Their ability to see crabs as small as 3 mm reinforces Wells' (1978) contention that cephalopods have excellent visual acuity. Their ability to handle large prey is no doubt a reflection of their great strength and flexibility.

12.4.5 Learning

With both *O. maorum* and *R. australis*, successive presentations of an acceptable prey resulted in an increased probability of further attacks and a decrease in their latency to attack. This modification of behaviour following experience is termed 'learning' and the same phenomenon has been documented for *O. vulgaris* (Boycott & Young, 1956) and *Sepia* (Wells, 1958). *O. maorum* and *R. australis* were capable of learning some associations on the basis of one experience only. Since 1950, an extensive series of studies has been made with *O. vulgaris*, assessing the ability of this animal to learn and discriminate (see Wells [1978] for a review). The task of the animal has usually been that of making what has been called classically a successive discrimination. Rhodes (1963) demonstrated that octopuses can effectively learn a direct simultaneous discrimination problem. Boycott & Young (1956) found that *O. vulgaris* is capable of learning not to attack if electric shock is administered as punishment. Boycott (1965) demonstrated that a normal octopus has a learning retention period of two weeks or longer. His tests of the octopuses' capacities before and after brain surgery support the idea that there were two kinds of memory: long-term and short-term. Short-term memory was *ca.* 30 min retention time. Their retention for learning not to attack lasted about 3.5 days.

In the laboratory, individual *O. maorum* and *R. australis* showed vastly different reactions to 'novel' prey. As these animals are capable of learning, it is feasible that these individual differences are attributable to differences in their 'ontogeny' or past experience during development. As none of my octopuses were laboratory reared, it was impossible to determine the relative role of learning on prey-attacks by these animals. There are few studies in the literature concerning the

ontogeny of feeding in cephalopods. Thomas & Opresko (1973) reared *O. joubini* and found that animals 2 - 21 days of age would not attack live food and that these animals could not be induced to eat *Artemia* at any stage. However, at 28 days *O. joubini* ate pieces of *Uca* appendages and suitably-sized live *Uca*. Wells & Wells (1970) studied newly settled *O. cyanea*, who in their second week after settlement made attacks on crabs. From that work Wells & Wells concluded that if not innate, the response to crabs or crab-like prey has been very thoroughly established by the time that *O. cyanea* settle on the bottom. In the cuttlefish, *Sepia*, the range of objects liable to evoke an attack begins by being exceedingly restricted but widens very considerably during the first week or so after hatching (Wells, 1958). There is, however, no change in the way prey were attacked, but the delay decreased with increasing presentations.

12.4.6 Prey Recognition

There are several theories concerning the possible systems of prey recognition. Given octopuses' ability to learn and retain discriminations, especially visual ones, it is possible that they learn specific features of every edible prey they encounter. However, this hypothesis requires that predators also have the ability to recognise a diverse number of objects in the environment as inedible. Robinson (1969) suggested that an alternative to individual recognition is that predators respond to common characteristics of a group of objects. That octopuses may do this is suggested by their preference for moving objects. Many objects, previously ignored, are immediately noticed if they move. It is also suggested by the possibility that these octopuses have an innate attack-response to 'crab' shapes.

Since octopuses, including *O. maorum* and *R. australis*, are capable of rapid learning, it will be necessary to guard against the effects of learning in the subsequent experiments with these animals. Consequently, it will be extremely important that the conditions are the same for all prey. They should only differ in the characteristic being determined: in this case, the presence or absence of the algal mask.

12.4.7 Familiarity of Prey

O. maorum and, in particular, *R. australis* selected crab types which they had previously captured in the laboratory. This preference for

familiar prey has also been found for the starfish *Acanthaster planci* (L.) (Ormond *et al.*, 1976) and for the kestrel *Falco sparverius* (Ruggiero *et al.*, 1979). Boycott (1954) reported that when exhibiting cautious behaviour towards a previously noxious stimulus, *O. vulgaris* paled on the side proximal to the prey and darkened on the distal side. He maintained that this bilateral colouration may have been indicative of an internal conflict. Bilateral colouration was marked in *O. maorum*, but it only occurred when these octopuses were stalking prey, and the side proximal to the prey flushed darker. As the background of the tank, especially the experimental tray, was darker than the octopus, this flushing probably served to make the octopus cryptic. In effect, it was a form of countershading akin to that found in sphingid larvae (de Ruiter, 1956) and as such would enhance the octopuses' stealthy approach.

12.4.8 Modes of Attack

Both parachute and tentacle modes of attack of *O. maorum* and *R. australis* were the same as those reported for other octopods. Parachute attacks were used predominantly when the prey were against a contrasting background, whilst tentacle attacks predominated when the prey were against a semi-natural matching background. This indicates that parachute attacks are visually directed. Maldonado (1964) found that the parachute attacks of *O. vulgaris* were visually oriented. He also found that light was not essential for the whole course of the attack. However, there was a minimum period of illumination, of a little less than one second, required.

12.4.9 Immobilisation and Ingestion of Prey

Boyle & Knobloch (1981) found that *Eledone cirrhosa* and *E. moschata* juveniles bored holes in a percentage of prey crabs (including 16.7% of the spider crab *Hyas araneus*) and then injected venom. *O. maorum* and *R. australis* do not damage the crabs until they have been immobilised, probably by the absorption of venom through the gills. Only then do they split the carapace and extract the contents.

12.4.10 Sensory Capacities of Cephalopods

The sensory capacities of *O. maorum* and *R. australis* could not be investigated. Since the majority of the behaviours investigated for the

New Zealand species were similar to those of other cephalopods, it is probable that their sensory capacities will also be similar. Accordingly, information on the sensory capacities of other cephalopods, which are relevant to the subsequent investigations, will be summarised.

Octopuses have an exceptionally good visual system, the eyes being the dominant sense organ in most cephalopod behaviour patterns (Young, 1956; Boycott, 1965; Boycott *et al.*, 1965; Russell-Hunter, 1968; Wells, 1978). However, *O. dofleini* appeared to be rather insensitive to changes in brightness (Autrum & Thomas, 1973). Virtually all the latest evidence suggests that octopuses lack colour vision (Hamasaki, 1968a, b; Messenger *et al.*, 1973; Roffe, 1975; Messenger, 1977b). Discriminations are based on absolute extents: they tend to classify shapes along a dimension that seems to depend upon the relation of outline to area (Sutherland, 1957a, b, 1961). Up and down movement was preferred to side to side movement (Wells, 1978).

Octopuses have complex chemo-tactile systems as well. *Octopus* can learn to distinguish objects by touch as readily and quickly as it can learn to distinguish between figures by sight (Wells & Wells, 1956). Physical differences between objects are distinguished in terms of the distortion they impose on the suckers with which they are in contact (Nixon & Dilly, 1977). Octopuses can not distinguish shapes, weights or sizes by touch (Wells, 1978) but they cannot learn to discriminate between objects which differ only in the arrangement of such irregularities or in the orientation of these relative to the form of objects (Gradziadei, 1971). Octopuses can also taste by touch, having chemo-tactile as well as mechano-tactile sensillae on various parts of the arms and suckers (Russell-Hunter, 1968). Wells (1963) found that octopuses can discriminate between sweet (sucrose), sour (hydrochloric acid), and bitter (quinine), and these substances can be detected in minute concentrations when dissolved in sea water.

Finally, the structure of the cephalopod brain (Russell-Hunter, 1968), coupled with the behaviour of these animals, suggests that octopuses are capable of short- and long-term memory.

SECTION II

CHAPTER 13

EXPERIMENTAL MATERIALS AND METHODS

Ideally, a study of the function of a behavioural character should be investigated in the natural context. Since *Notomithrax ursus* and the intended predators, octopuses, are cryptic (to human observers), nocturnal, and marine, even brief field observations were impossible. The bright light and close proximity of the observer necessary for such observations had adverse effects on the behaviour of both the predators (Chapter 12; also Woods, 1965; Altman, 1967; Yarnall, 1969; Kayes, 1974) and prey (Chapter 8). Also, underwater observations at night are particularly dangerous in rocky intertidal areas. In the case of many species such problems have been overcome by the use of the capture-release-recapture technique whereby animals possessing variations of the character in question are released in a certain area (e.g., Kettlewell, 1956). As *N. ursus* begins masking immediately the mask is removed, it was not feasible to do a capture-release-recapture study.

Consequently, since it was impossible to collect sufficient data in the field, the function of the algal mask was investigated by studying the interaction between *N. ursus* and octopuses in the laboratory under strictly experimental conditions, with little reference to the extant field conditions. This form of approach has the advantage that variables are controllable and may be altered one at a time, greatly increasing the probability that results can be confirmed by others.

13.1 ANIMALS USED

13.1.1 Crabs

The general collection, transporting and housing of all five species of crabs used in this section of the study was the same as outlined in Chapter 3. These procedures followed the guidelines suggested by Jackman (1968).

(a) *Notomithrax ursus*

In the laboratory, *N. ursus* were housed in the Type 1 and 2 tanks and provided with algae consisting mainly of clumps of *Halopteris spicigera*. The number of crabs/tank (6 - 25) depended on the size of the individuals concerned. While not actively involved in the experiments, crabs were kept under the aquarium room lighting (i.e., 12 h light : 12 h dark normal photoperiod). When exposed to a reverse 12 h light : 12 h dark photoperiod the crabs adjusted within 5 min.

With *N. ursus*, the character in question was the mask and a difference was obtained by comparing crabs which had all body areas covered with algae (= masked) with crabs that had the algae removed from all body areas (unmasked). The mask is an excellent character for the study of function for several reasons. A difference could be obtained simply and quickly by using fine forceps to pluck the algal pieces from amongst the hooked hairs, and the absence of the mask did not result in any observable changes in any other characters (Chapter 8). As newly moulted crabs required a maximum of 48 h to completely re-mask, and moulting occurred for 9 months of the year, the comparison morph (lack of mask) was not unnatural for the species.

Masked crabs were individuals that had the entire dorsal surface of all leg segments and the carapace covered with *H. spicigera*. As masked crabs have a larger outline, to the human eye, than unmasked individuals, masked crabs were always of a slightly smaller size than the corresponding unmasked crabs. Sizing was determined by measuring the carapace length of crabs and then matching the overall area by eye. In some experiments the numbers of crabs required prevented their being matched for sex. In these particular cases, results were analysed to check for the effects of sex difference. Unless stated, the effect of the mask was not altered by the sex of the crab.

(b) Non-masking crabs

In Chapter 14, two species of non-masking crabs, with smooth hairless exoskeletons, were used to compare the reaction of octopuses to masking and non-masking crabs and to provide a comparison between the anti-predatory behaviours of these two classes of crabs. *Petrolisthes elongatus* and *Hemigrapsus edwardsii* were chosen as, intertidally, they

inhabited the same areas as *N. ursus* and hence in the field possibly provided a weakening of the effects of predators on *N. ursus*. These crabs were always collected from the same areas as *N. ursus* and were transported and housed in the same manner. The only exception being that they were not provided with algal clumps. As these crabs were of a different body shape to each other and to *N. ursus* they were size-matched for trials by using the body area (i.e., cephalothorax length times width).

13.1.2 Octopuses

The data concerning the species, sexes, sizes, and areas of capture of the octopuses used in this section can be found in Table 12.1 (Chapter 12). Octopuses were obtained from the intertidal region and from deeper waters by the local fishermen who occasionally caught them in crayfish pots and set nets. As this study was concerned with *N. ursus* populations from the intertidal area, octopuses from this area were used in preference to those from deeper water. Where possible, octopuses were hand-netted, whilst moving in open water, during catching and at all subsequent handling times, to minimise the risk of stress. Large, soft-bristled brushes were found to be very effective in coaxing animals to required positions and although these brushes were avoided by the octopuses they caused no apparent harm.

Octopuses were transported singly in the same manner as crabs (Chapter 3). The ice lowered the water temperature to below the 8°C necessary to keep the octopuses inactive. Upon arrival in the Zoology Department aquarium, the 'bagged' octopuses were placed in the circulating sea water system until the respective water temperatures had equilibrated. The animals were then tipped into their holding cages (Fig. 13.1) which were designed to cater for several requirements. Preliminary observations demonstrated that both *Octopus maorum* and *Robsonella australis* required a certain minimum living space, supplied with well-oxygenated running sea water. The only suitable place in the Zoology Department aquarium was the overflow tank ("sink") to the circulating sea water system. Since other researchers (Taki, 1941; Boycott, 1954; Lane, 1960; Woods, 1965; Wells, 1978) had found octopuses to fight to the death, they had to be kept singly. The construction of these plastic mesh cages meant that five to six octopuses could be housed at one time without any harm coming to them. Joining the mesh to form a

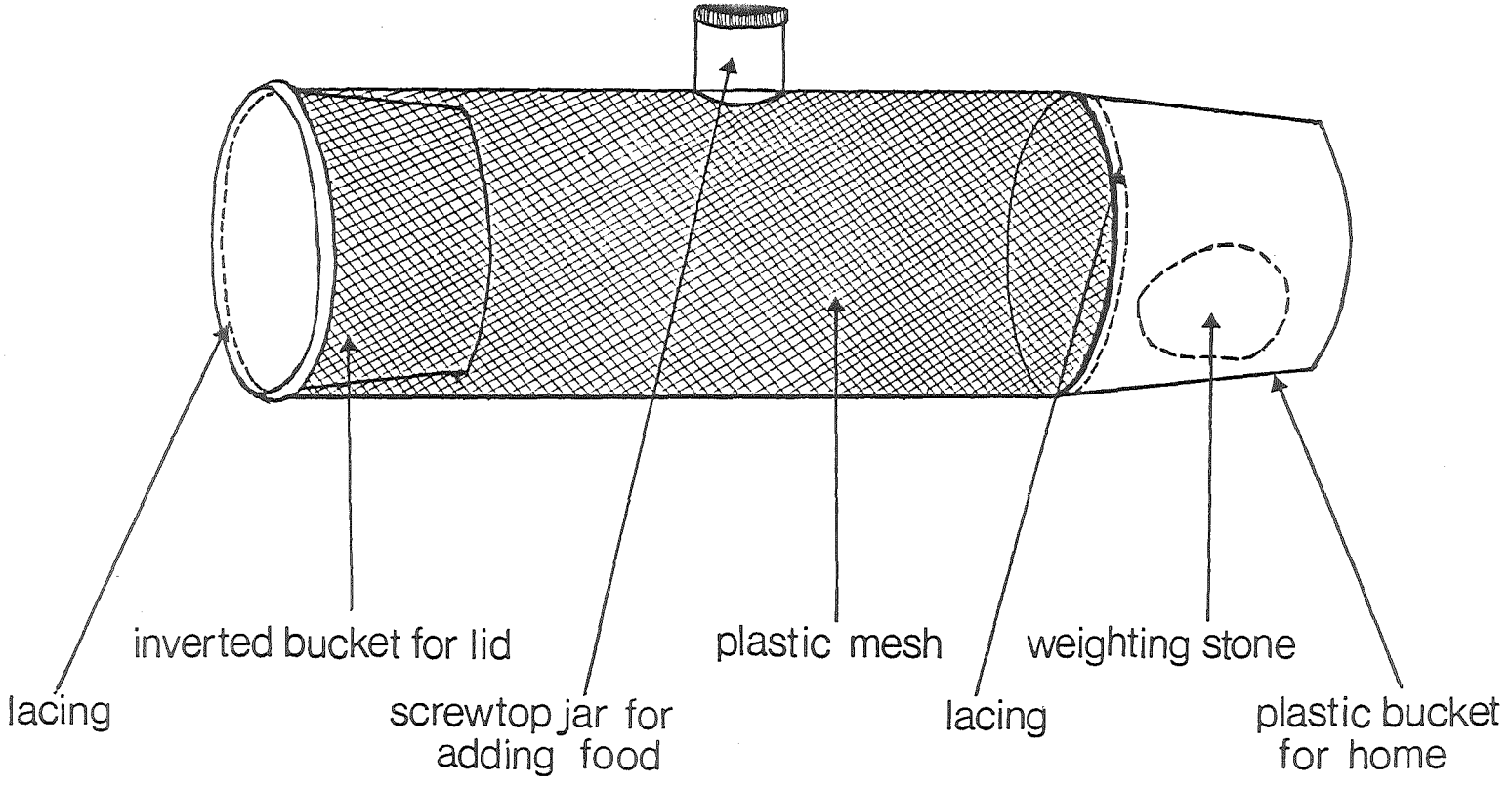


Fig. 13.1 Holding cage used to house individual octopuses prior to experimentation.

tube, double-lacing it together and then lacing a bucket at either end, ensured that these animals could not escape. One bucket, placed so that its bottom surface faced into the tube, formed a lid and ensured the octopus could not force its way through the lacing. The other bucket, with its bottom surface facing out from the tube, provided the octopus with a dark refuge. The addition of a large stone gave the octopus the necessary thigmotactic stimulation and also provided weight to keep the cage on the floor of the overflow tank. The use of fine plastic mesh, while not preventing a good flow of water, made it difficult to see into the cage and effectively discouraged annoyance from interested observers. The top part of a plastic screw-top bottle was welded to the edges of a small hole cut in the mesh, allowing food to be put into the cage. The octopuses were fed with *Hemigrapsus crenulatus* crabs which were readily available locally in the Christchurch estuary.

These cages were extremely successful as octopuses could be kept healthy for at least six months and, of the 26 individuals retained in this manner, only one very small female (100 g) managed to escape. She survived as she escaped into the large volume of well oxygenated water in the overflow tank.

13.2 EXPERIMENTAL AQUARIUM

This aquarium and subsequent additional pieces of apparatus were designed and prepared in accordance with the guidelines for aquarium construction as stated by Mariscal (1974) and to satisfy the requirements necessary for keeping crabs and octopuses healthy, as outlined by Jackman (1968). The tank measured 118 x 57 x 28 cm and was constructed of kauri marine ply with a glass viewing panel inset in one side. The wood was coated with 'Evidure Timber Preservative' and 'Epiglass Resin and Hardener' held together with 'Urea Formaldehyde Resorcinol 521' glue. All of these substances were non-contaminating. Sea water was supplied, through P.V.C. tubing, from the main circulating system. Following Boycott's (1954) recommendation, the inflow and outflow pipes were glued in place to prevent inquisitive octopuses from dislodging them. Since octopuses require well-oxygenated water, the tank was equipped with stone bubblers for additional aeration.

One difficulty in experimenting with octopuses stems from their resistance to being moved from their living tank to a piece of experimental apparatus. This difficulty was overcome by housing the animals in the experimental aquarium for the duration of their time as subjects. This method, which requires one set of apparatus for each animal being studied at any given time, has previously been used quite satisfactorily by Maldonado (1964), Wells (1964), and Walker *et al.* (1970). The interior of the tank could be divided into living and experimental sections by removable perspex partitions. Drilling tiny holes in the perspex meant that the water flow was not impeded. These dividers were raised and lowered by a pulley system engineered so that any attached divisions could be moved simultaneously (Fig. 13.2). One section, the home area, contained a home made of three bricks one atop the other two. The size of this home could be varied to suit the size of its current inhabitant. These bricks were always scrubbed in hot water before being used for a different octopus.

For experimental efficiency, two octopuses were used simultaneously. Only one octopus was in its experimental area at one time and the distance between its experimental area and the other animal's home area was sufficient to prevent their disturbing each other.

To prevent the octopuses excavating holes amongst the rocks and the crabs from moving away from the rocks, effectively changing their background, removable trays were made to keep the rocks and algal clumps in place. These trays, which fitted neatly into the experimental areas, had the floor and two sides made of wood, and the third side and the lower part of the front (fourth) side made of transparent perspex. The removable trays enabled the arrangement of three different conditions.

Matching background

Algal covered rocks, taken from the same area as the experimental crabs, were placed in the tray so that they sloped gently up and back from the top of the front perspex. The inter-rock spaces were filled with pea gravel to prevent the crabs hiding. A clump(s) of *Halopteris spicigera* was secured between the rocks so that one-third of the tray was covered by the algae. This situation closely approximated the natural conditions when *N. ursus* were exposed to predators. The outline of the crabs was made less conspicuous by painting the wooden sides black.

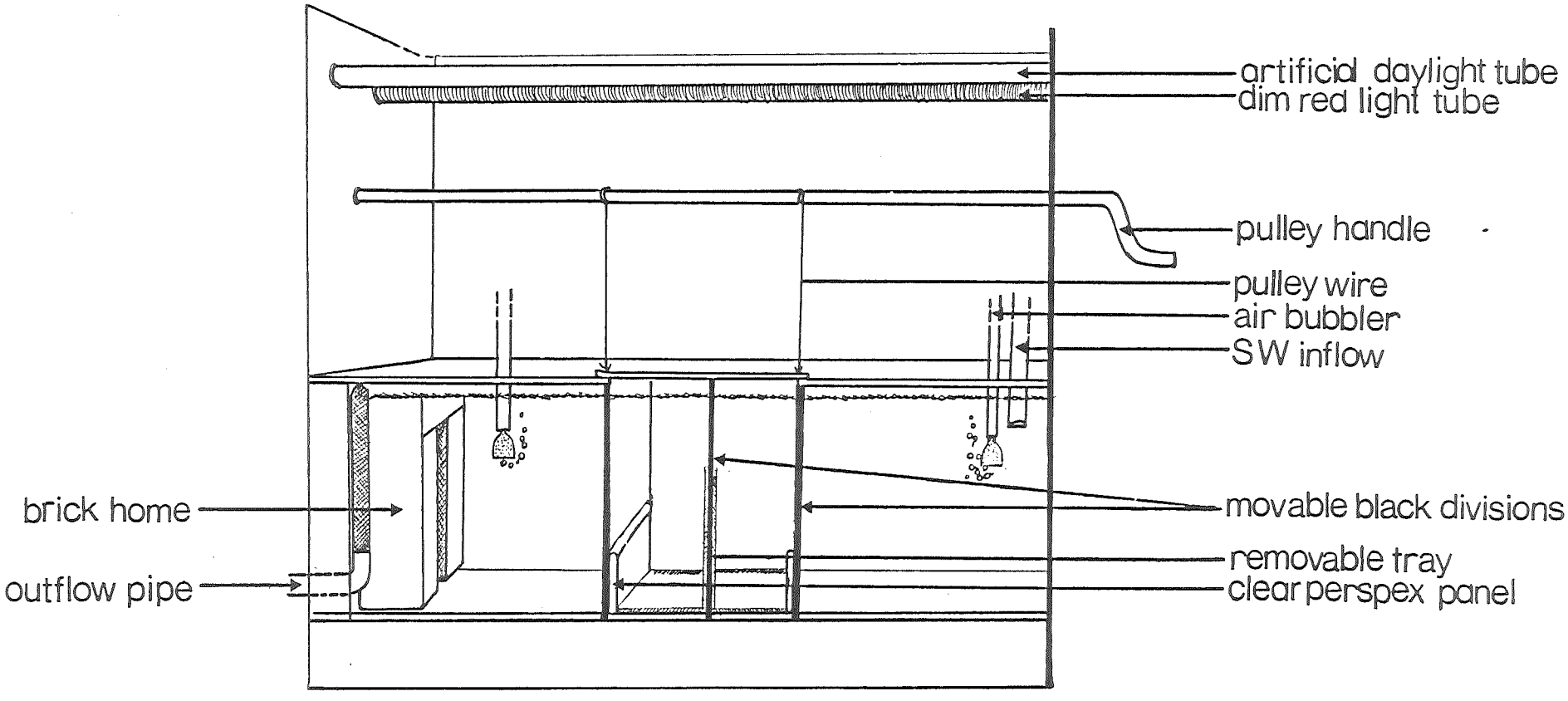


Fig. 13.2 Schematic representation of the experimental aquarium showing the lighting, pulley and division systems, removable trays, and home and experimental areas.

Contrasting background

Covering the floor and wooden sides with smooth white perspex ensured that the crabs were visually, texturally, and chemically exposed to the maximum extent.

Other species background

This was the same as the matching background but an individual from each of two taxonomically different non-masking species, *Petrolisthes elongatus* and *Hemigrapsus edwardsii*, was also offered.

To prevent the octopuses from escaping, the tank was supplied with transparent perspex lids which were screwed to the tank. The lid was composed of three interlocking sections so that access could be gained to the experimental areas without the octopus escaping from the home area.

With the exception of the water supply, the experimental aquarium was an independent unit. This was achieved by totally enclosing the tank within a pinex chipboard and black polythene hide (Fig. 13.3). During experiments animals were prevented from seeing the observer by the use of removable blinds. The combination of the hide and blinds ensured that prior to and during experimental trials the octopuses were guarded from disturbance. Some human intervention after each trial was unavoidable as uneaten crabs had to be removed.

Since *N. ursus* were extremely photonegative (Chapter 8) and were probably only exposed to predators at very low light intensities (Chapter 7) and octopuses, although opportunists, were primarily nocturnal hunters (Chapter 12), it was necessary to conduct the observations and experiments under simulated night time conditions. Since observations were to be undertaken for three years, but the experimental animals would only be used for brief periods (crabs: max^m 48 hours; octopuses: max^m three months), it was decided to reverse the animals' activity cycle rather than the experimenter's. Octopuses required only 3 - 5 days to reverse their diurnal cycle and none of the subjects exhibited any measurable changes in behaviour after having their diurnal cycle reversed.

A reverse 12 h light : 12 h dark photoperiod was provided by fluorescent tubes, suspended 53 cm above the water surface of the

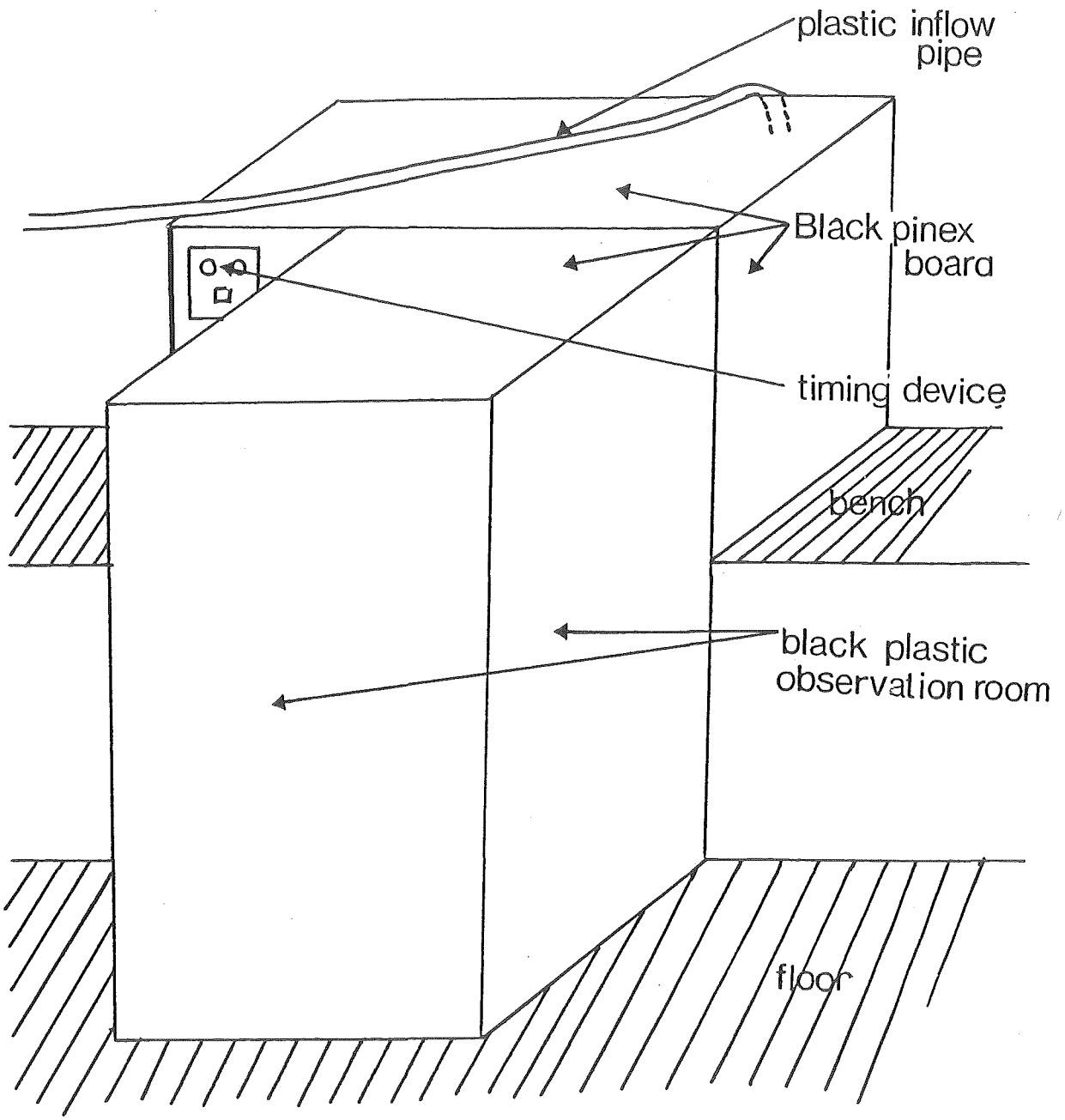


Fig. 13.3 Observation room enclosing the experimental tank.

experimental aquarium. Daylight was approximated by a 'Thorn Artificial Daylight 65 W' fluorescent tube (Fig. 13.4 for spectral distribution). Since it was always necessary to observe the interactions between *N. ursus* and *O. maorum*, the experiments could not be conducted in the very dim light afforded by starlight or even moonlight. Hence, darkness was provided by a 'Thorn Red 65 W' fluorescent tube (spectral distribution 575 - 750 nanometres, Fig. 13.5). Narrow band red light was specifically chosen for several reasons. Firstly, as red light is absorbed close to the surface, the intensity was likely to be even lower under water. Secondly, crabs (Chapter 8) and octopuses (Messenger *et al.*, 1973) are reported to have impaired vision at these wavelengths. Also, octopuses are reported to have a similar absorption spectra to humans (Messenger *et al.*, 1973) and when viewing through the side of the aquarium, the experimenter could only just observe all the details of the various interactions.

In this study, light intensity was measured using an electronic submarine light meter constructed by University of Canterbury technicians. This meter was calibrated in foot lamberts (1 foot lambert = $\frac{1 \text{ foot candle}}{1 \text{ steradian}}$) which is a measure of radiance, N. Although experimentalists most commonly have used foot candles (ft.c) or metre candles (mc, also called lux) and occasionally millilamberts (mL), which are measures of illumination, these units should be avoided (Segal, 1970). Measures of radiance and measures of illumination are not directly comparable. However, to provide some measure of comparison the approximate conversions to foot lamberts have been marked in Fig. 13.6, which also shows light intensity, in air, in metre candles associated with different types of natural light.

Since the aim of measuring the light intensity was to gain a comparison between laboratory and field conditions, the units used were not of critical importance. However, a problem arises in that light intensity in the field is affected by the depth and clarity of the water, the season, weather, and time of day. Another problem is that the reflection of light from the surfaces of experimental tanks may be as important as the incident light in determining the state of adaptation of the eye. Consequently, the light intensities obtained underwater in the laboratory under the artificial daylight, red light, and the red light screened by four layers of 2 mm^2 plastic mesh are compared to various

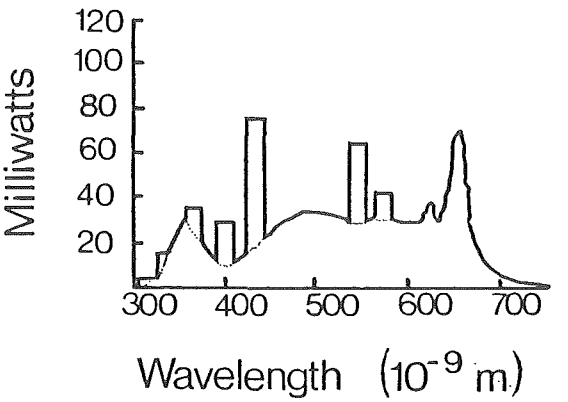


Fig. 13.4 Spectral distribution of the 1500 mm, 65 W 'Thorn' fluorescent tube used for artificial daylight used in experimental conditions (after the 'Thorn' catalogue).

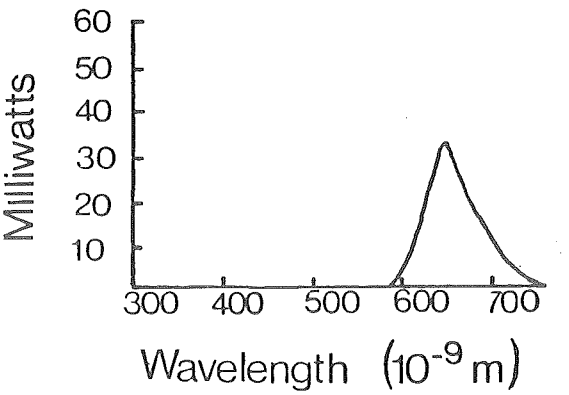


Fig. 13.5 Spectral distribution of the 1500 mm, 65 W 'Thorn' fluorescent tube. Used for dim red light used in experimental conditions (after the 'Thorn' catalogue).

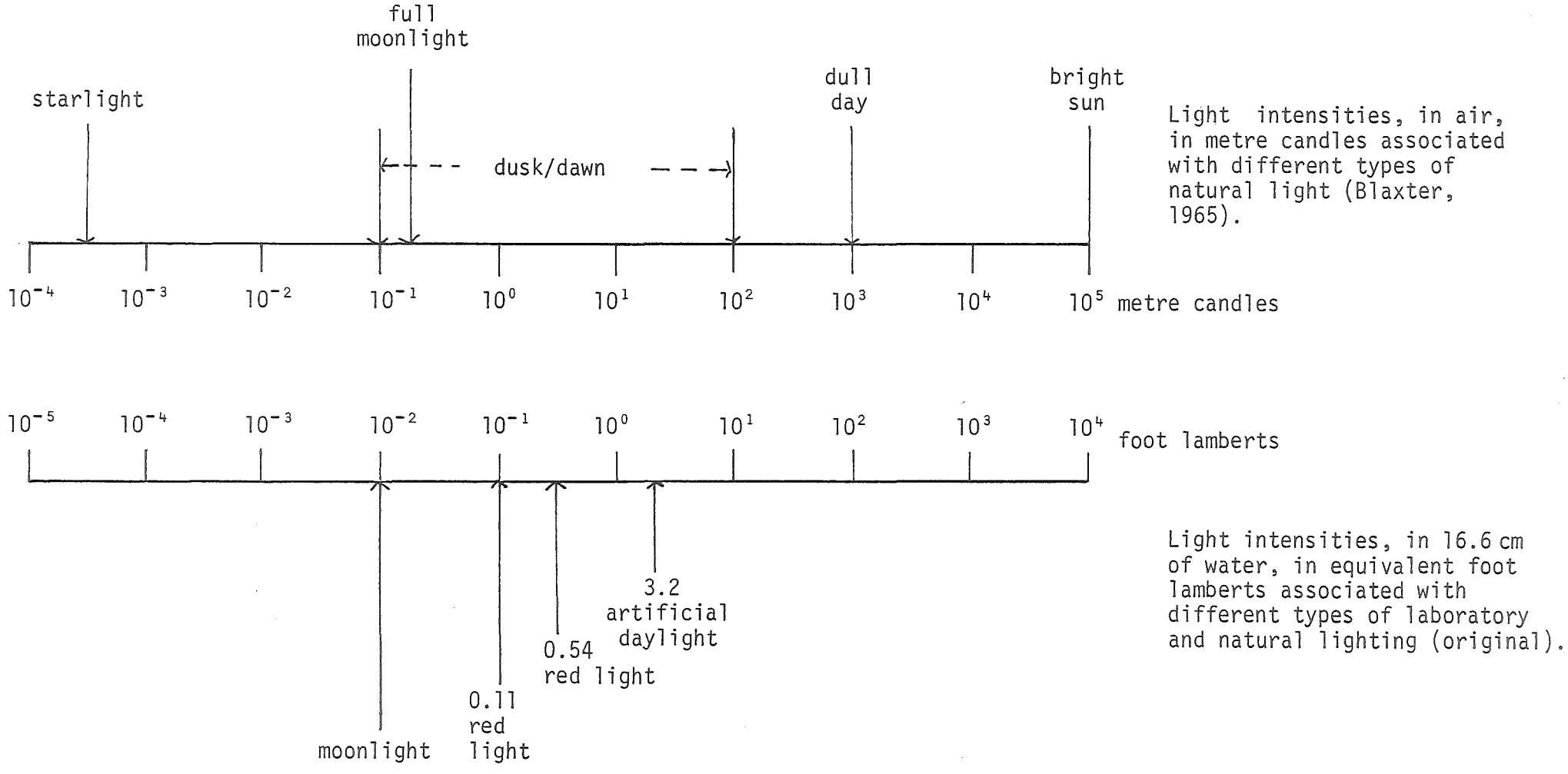


Fig. 13.6 Comparison of light intensities in foot lamberts associated with natural and laboratory lighting with 'equivalent' metre candles.

readings underwater in the field in Table 13.1. These readings have also been indicated on Fig. 13.6. As noted previously, laboratory "darkness" was brighter than nocturnal conditions in the field even on a full moonlight night. However, if the mask is effective at deceiving a predator at a particular intensity, say 0.11 foot lamberts, then it is reasonable to assume that it will be even more effective at intensities lower than 0.11 foot lamberts.

13.3 METHODOLOGY

After a 3 - 4 day quarantine period to check that it was healthy and feeding, an octopus was transferred to the home area of the experimental aquarium. The animal's behaviour of returning to this home at frequent intervals, especially to feed, provided a suitable way of ensuring that an individual was always in the same place at the beginning of a trial. An octopus was confined to this home area until it had reversed its activity rhythm. During this adjustment period it was fed with *Hemigrapsus crenulatus*. Following adjustment the octopus was permitted to explore and become familiar with the experimental area. If any additional pieces of equipment were used the octopus was always allowed time to explore and become familiar with these.

As several factors affected the octopuses' propensity to hunt, these animals were subjected to trials only if they were showing appetitive behaviour (Chapter 12). This avoided distortions due to low motivation, as only data from periods when the predator was ready to hunt were considered suitable.

Randomly positioned control trials were used to ensure that the octopuses were reacting to the crabs and not to extraneous cues such as the raising of the partition. These trials were identical to the experimental ones but no crabs were presented. To lower the effect of possible extraneous cues, exactly the same procedure was followed, from preparation to conclusion, for every trial of a given experiment.

Behaviour was recorded on a tape recorder for later manual analysis of the frequency of actions performed by the predators and the sequence in which they occurred.

Table 13.1 Light intensities, at varying depths, in the laboratory and in the natural habitat, Kaikoura Peninsula. Natural moonlight measured with red cellophane over sensor.

Depth (cm below water surface)	Light intensity (foot lamberts)			
	Experimental tray			Kaikoura shore
	Artificial daylight	Red light	Red light and four layers 2 mm mesh	Moonlight
0	5.0	0.74	0.13	0.01
16.6	3.2	0.54	0.11	0.01
28.6	2.2	0.32	0.06	0.01

SECTION II

CHAPTER 14

THE INTERACTION BETWEEN *NOTOMITHRAX URSUS* AND THE PREDATORS *OCTOPUS MAORUM* AND *ROBSONELLA AUSTRALIS*

14.1 INTRODUCTION

Previous results (Chapters 9 and 12) were ambivalent concerning the effect of the mask on predation of *N. ursus* by octopuses. Preliminary work in Section II Chapter 12 revealed that predatory interactions between octopuses and crabs are comprised of complex sequences of behavioural events. Consequently, merely considering which crabs were ingested and not the sequence of the predatory interaction nor the order of reaction to the crabs, would make a determination of the effect of the mask unlikely. Hence, the aim of this chapter was to describe and analyse in detail the interactions between masked and unmasked *N. ursus* and predatory octopuses to ascertain at what point, if any, the mask had an effect.

Initially, a comparison of the reactions of octopuses to masked and unmasked crabs was made in a simulated natural environment (henceforth referred to as 'matching') to determine whether the algal mask has any noxious or toxic properties, consistent with the hypothesis that the mask may have an aposematic function, or whether the mask has a procryptic function. However, this comparison did not make it possible to determine whether the mask functions as eucrypsis or special protective resemblance. *N. ursus* should be confused with the inedible regardless of the background if the mask is special protective resemblance but not if it is eucrypsis (Turner, 1961; Robinson, 1969). Consequently, the crabs were also presented against a non-matching background (henceforth referred to as 'contrasting').

Section I failed to provide evidence of the importance of *N. ursus* as a prey animal, or even that they were a natural prey of octopuses. Cephalopods are known to display different predatory behaviours with different prey types (Neill & Cullen, 1974). Given that *N. ursus* is a natural prey of octopuses, is *N. ursus* hunted as 'crab' type prey or as

"non-crab" prey? Are masked individuals treated as "non-crab" prey whilst unmasked are hunted as "crab" prey? Very few animals rely on only one line of defence; they usually possess secondary defences and also behaviours which are supportive of these primary defences. Does the mask require special behaviours to achieve and maintain its effect, and are these behaviours different from those shown by non-masking crab species? These questions can be answered by studying analogous predatory interactions between octopuses and species of non-masking crabs in a simulated natural environment (henceforth referred to as 'other species').

14.2 MATERIALS AND METHODS

14.2.1 Experimental Aquarium

The experimental aquarium, described in Chapter 13, was used, the removable trays being set up with a matching, contrasting, or other species background, depending on the requirements of a particular bracket of trials.

The lighting was still on a reverse daylight regime but the ratio was periodically altered to maintain parity with external conditions.

14.2.2 Animals Used

Nine octopuses (numbers 9 - 17, Table 13.1) were used of which five (two *R. australis* and three *O. maorum*) contributed the majority of the data, while one *O. maorum* contributed very little data.

Because of the difficulty of observing more than four crabs at once, only one masked and one unmasked crab were presented at each trial and, in the 'other species' situation, one *Hemigrapsus edwardsii* and one *Petrolisthes elongatus* were also presented. All crabs were matched for size of the carapace area, but not for sex.

14.2.3 Procedure

A previously quarantined octopus was introduced into the home area of one half of the experimental aquarium. When adjusted to both its surroundings and the reverse light regime the octopus was fed with two *H. crenulatus* and left for 24 h. The tray was then inserted in the

experimental area and remained in position until all trials in that particular block were completed. A tray was removed during a run only if the octopus refused to leave it, or if a crab managed to excavate under the rocks.

In each experiment, the prey were introduced into the experimental area of the tank by tipping them gently out of a water-filled beaker, lowered from the observation position to one side of the tank and so that the predator could not observe this process. The same procedure was used for every trial and the crabs were placed so that they were equally exposed and equally accessible to the octopus. As octopuses react best to moving stimuli, the division between the experimental and home areas was raised immediately following the addition of crabs to make the maximum use of their settling down period. This strategy enabled more data to be collected on immediate attacks by the octopuses.

Recording began immediately the division was raised and continued until the predator lost interest for 5 min or until no prey remained. However, all trials lasted a minimum of 15 min. A note was made of every act performed by the animals and the reaction(s) each act elicited. The exact times at which each act occurred were also noted.

The octopuses were tested singly, trials continuing until each had made ten attacks (or had ten consecutive trials without making an attack), then the environmental conditions were changed. A one-day interval was allowed between test-sets with the differing backgrounds and each new set began with a control trial to lower the novelty effect of the different appearance of the tray. The order in which the three environmental conditions were presented was randomised to prevent any sequential effects or learning.

Since the octopuses died unpredictably, it was not possible to equalise the number of crabs actually eaten, or even attacked by each octopus. Because of the difficulties of obtaining and keeping the octopuses, and as they showed individual differences in their responses to the various experimental conditions, each animal was exposed to as many trials as possible, still altering the backgrounds every ten attacks.

Some octopuses did not consume their captures. Since starved octopuses cease hunting (Chapter 12), these individuals were fed one

H. crenulatus, in the *home* area, every second day ensuring that they continued to hunt during the experimental trials.

14.2.4 Analysis

(a) Behaviours considered

To determine the effect of the mask it was first necessary to make an 'ethogram' of the predatory behaviours of the octopuses and the anti-predatory behaviours of *N. ursus* involved in the interactions. Although partial repertoires had already been gained for crabs (Chapter 8) and octopuses (Chapter 12) each catalogue needed to be an exhaustive and exclusive classification. Following Altmann (1965) the continuum of action was broken wherever the animals broke it, in an effort to recreate natural units of predatory/anti-predatory behaviour. As the termination of one behaviour sometimes came after the initiation of the second one, scoring of these sequences was based on the onset of the actions.

Once the predatory ethogram was completed, the predatory sequences were determined. A 'sequence' began when a prey was detected and ended when the octopus started ingesting the prey or the prey escaped. The sequences had to progress forwards, i.e., they could not recycle. The point of re-entry automatically constituted the beginning of a new sequence. As it was impossible to ascertain if a stimulus was not detected, events prior to the octopus orienting to the stimulus were excluded. In the majority of cases it was impossible to determine whether a defensive behaviour was given in response to the octopus or another stimulus (e.g., another crab). Accordingly, only defensive behaviours exhibited when the crab was touched by the octopus were considered. As the most important prey stimulus to octopuses is movement (Chapter 12), the crab's defensive behaviours were grouped into 'moved' or 'immobile' for the sequence analyses. Several sequences had to be excluded from the analysis because relevant actions were not fully distinguishable. Certain behaviour patterns occurred very rarely and these were grouped with other similar acts. For example, the octopus generally oriented by turning its head and arms in the direction of the stimulus. However, it occasionally reacted only by lashing out in the direction of the stimulus with a tentacle. Both these behaviours were considered as 'oriented'. Some sequences were deleted because they occurred so rarely that they provided insufficient data for statistical testing.

(b) Data presentation

In accordance with Robinson & Olazzarri (1971) and others, a model of the interactions between predatory octopuses and *N. ursus* was constructed. The diagram used to illustrate the behaviour sequences (Fig. 14.1) shows the basic units of behaviour connected by arrow-headed lines. The arrows indicate the direction of change from one behaviour to another.

As the frequency counts were based on the onset of patterns not their duration, the probabilities provide only an indication of the likelihood of any pattern following a given event, but not at any particular instant in time. It is also important to remember that each diagram is a summary of trends and does not allow individual sequences to be followed.

(c) Analysis of sequences

To examine how the octopuses' hunting success is affected by the mask and the differing experimental conditions, the data were analysed using the sequential contingencies among behavioural events. The most casual observations quickly revealed that all patterns of behaviour were not equiprobable and hence stochastically independent so the zero-order approximation was abandoned. Instead, following Altman (1965) and in accordance with the recommendations of Slater (1973), I obtained estimates of the probabilities p(K) of each behaviour pattern (K), i.e., a first-order approximation. So, for a particular act in the sequence of an interaction, say 'detects stimulus', the number of occasions when the next act was a 'direct attack' was totalled up and divided by the total number of times a stimulus was detected. The same procedure was repeated for the number of times 'detects stimulus' was followed by 'need more information' or resulted in 'no further response'. Fig. 14.2 illustrates the results of this analysis for masked crabs in the matching background.

Having derived the transition probabilities between each stage and its following act, the effect of the crab type (masked, unmasked, *H. edwardsii* and *P. elongatus*) and background (matching, contrasting, and other species) on the predatory behaviour of octopuses was tested using the likelihood ratio (G) test of independence where $n > 200$ and the G_{adj} test where $n < 50$ (Sokal & Rohlf, 1969).

14.3 RESULTS

The predatory sequences that occurred fell into five stages. Each stage was followed by two or more pathways which led to the formulation of a model which incorporated 'stimulus levels'. These levels were indicated by the behaviour which followed them (Fig. 14.1).

The first stage was Prey Location where the octopus detected the stimulus from a distance, the overt response being orienting to the stimulus. After locating the prey, the octopus exhibited one of three behaviours.

No further response (NFR)

This was shown by a loss of interest in the stimulus and the octopus changed to a non-predatory behaviour or entered the uninterested position. Since the octopus appeared to receive insufficient information to arouse any further response, the stimulus level was considered 'Low'.

Attack (A)

The octopus immediately parachuted the crab. As parachuting occurs only when the octopus is not hesitant about the stimulus (Chapter 12), the stimulus level was considered 'High'.

Tentacle probe (TP)

The octopus touched the crab, often repeatedly, exploring it. Since the octopus resorted to using proximal cues, it appeared to require more information. Consequently, the stimulus level was regarded as intermediate.

Touching the crab constituted the second stage, that of Prey Discrimination. This stage depended on the prey's behaviour: the crab either moved or remained motionless (Chapter 8). Movement was any motion except maintenance movements (e.g., of the mouthparts). In turn, the octopus either gave no further response or tentacle attacked. Accordingly, the proximal information received was considered 'insufficient' for attack in the former case and 'sufficient' in the latter case. Sequences could begin at this level as a result of the octopus contacting the prey without prior orientation to the prey (referred to as a non-oriented contact).

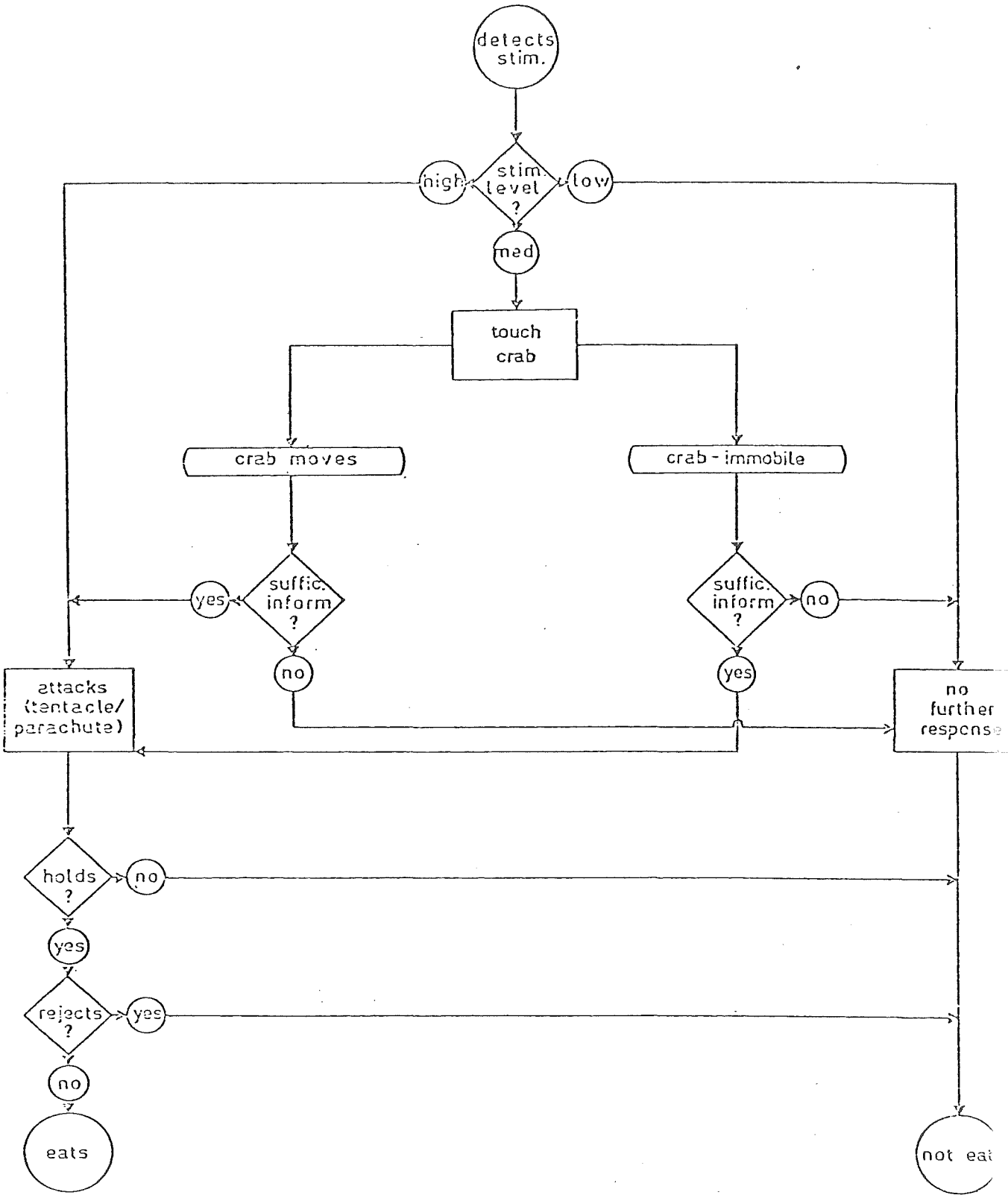


Fig. 14.1 Simplified model of the interaction between a predatory octopus and *Notomithrax ursus* (under laboratory conditions).

Once the octopus had attacked (by either method) it clamped the suckers on to the prey and the third stage, Prey Immobilisation, was reached. Additional information on the attacks made was gained by incorporating those sequences where the prelude to attack could not be determined.

If the prey could be held, the sequence entered the fourth stage, Prey Transportation, where the crab was actively accepted or rejected.

If the crab was accepted, the fifth and final stage of Feeding occurred. At this stage the octopus entered the eating position. It is important to note that prior to this phase the crab suffered no harm, albeit the occasional loss of a limb or, more commonly, the loss of some algal pieces.

All results and consequent comparisons in this study were based on the pooled data from the nine octopuses. This was a necessary step to obtain statistically testable numbers in the majority of areas. Although all nine octopuses exhibited wide individual differences, the trends for each octopus were all in the same direction, only the strength of response varying in each case. In all comparisons the data for each octopus were tested for homogeneity by the G_H test. The octopuses differed in only one area, the eat/not eat comparison. This was a species difference and the data were treated separately.

14.3.1 Masked Crabs with a Matching Background

The masked crab was eaten in only 11.87% of the 219 sequences (Fig. 14.2). As octopus is reported to be an efficient predator of other crabs (Chapter 12), where, in the predatory sequence, were *N. ursus* gaining this immunity from harm?

An examination of the probabilities at each stage of the model revealed that the zero-order approximation (i.e., the equiprobable model) did not hold true for the *N. ursus* - octopus interactions.

When perceived at a distance these crabs had a very low probability of being immediately attacked. Only 3% of those detected provided a sufficient stimulus level for the octopus to make an immediate attack (Chapter 12). Of the crabs detected, 36% elicited no further response from

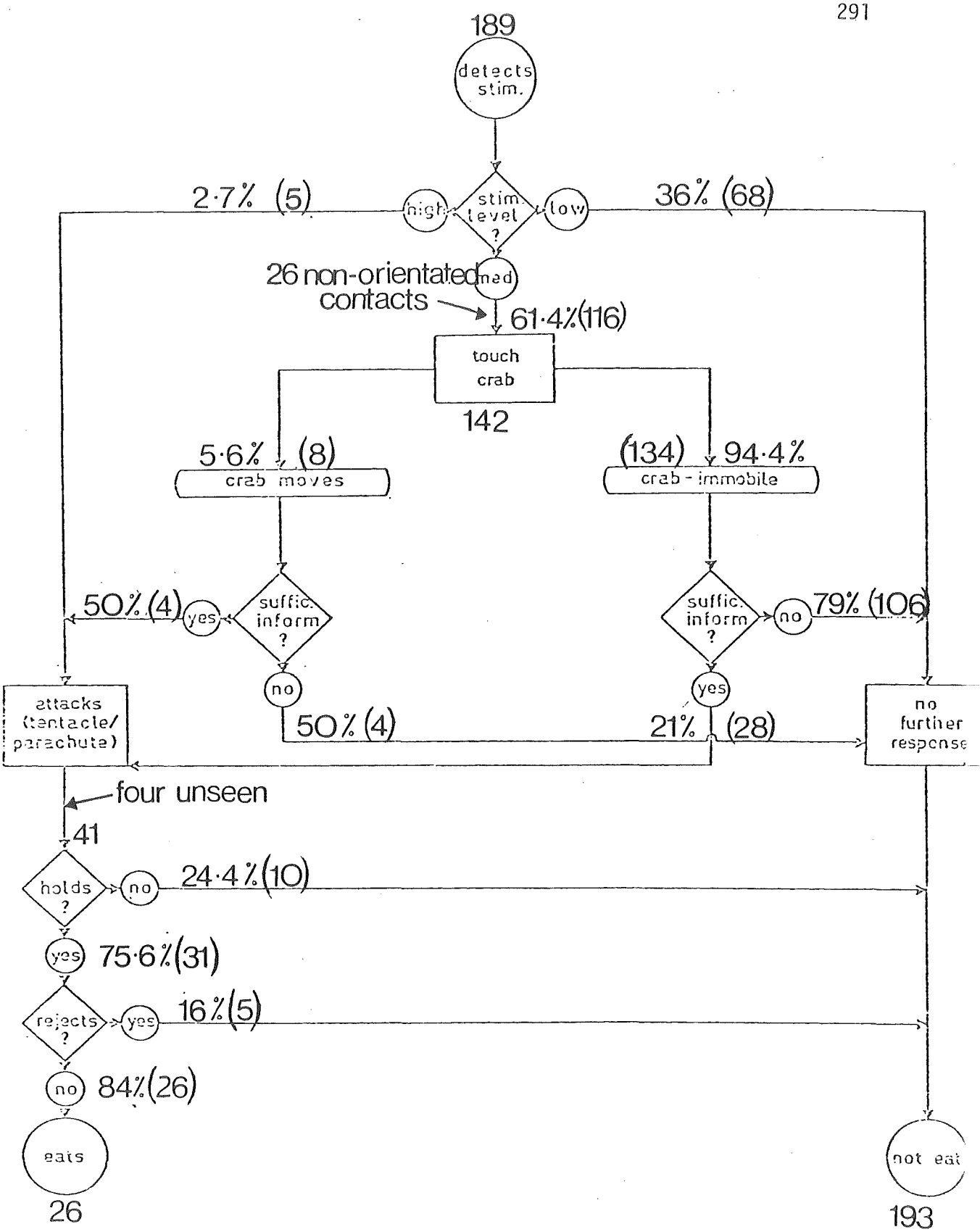


Fig. 14.2 Simplified model of the interaction between a predatory octopus and masked *Notomithrax ursus* (under laboratory conditions).

the octopus. In nature, the octopus would probably have moved on to another area, but in this laboratory situation, it either waited for another stimulus or it lost interest completely. However, the majority of crabs (61%) elicited uncertain behaviour (Chapter 12), the octopus seeking further information by tentacle probing. Hence, 97% of masked crabs perceived from a distance had some attribute(s) which inhibited, or confused, the orientation, or triggering, of an attack by octopuses.

Once contacted, the majority (94%) of crabs ceased all but respiratory movements. Of these immobile crabs, 79% failed to elicit any further response and hence escaped from that particular encounter. So, the most common sequence consisted of the octopus detecting a distant stimulus, then seeking further information by touching the crab which immediately stopped all movement resulting in the octopus making no further response.

As octopuses generally attack moving objects, one would expect most of the crabs who moved when touched to have been attacked. This was not found to be the case; 50% of the moving crabs were ignored. However, the results may well have been a result of the small sample size (n = 8).

Even after an attack the crabs still had a chance of survival; 36% being discarded unharmed. Analysis of grouped data revealed that the octopuses failed to immobilise 24% of the crabs attacked. However, an examination of the individual results showed that these failures were all attributable to one octopus, No. 13. If the results from this octopus are disregarded, 100% of attacked crabs were held. Of those crabs retained, 16% were rejected physically unharmed. There was no evidence of caution or reluctance to eat the remaining 84% of those crabs attacked.

Hence, once the crab was attacked, the most common sequence was for the crab to be held then eaten.

An examination of the probabilities at each stage of the model indicated that *N. ursus* was protected at several stages. It now remains to determine what factor(s) was responsible for this protection from octopuses. For ease of comparison, the effects of the algal mask, contrasting background, and the presence of non-masking crab species were dealt with for each stage.

14.3.2 The Percentage of Detected Crabs Eaten

The mask made no difference to the percentage of detected *N. ursus* eaten in all three experimental conditions. In addition, as many detected crabs were eaten against a contrasting background as against a matching background (Table 14.1).

Table 14.1 Percentage of crabs eaten of those detected from a distance.

Background	Crabs			
	Masked *N. ursus*	Unmasked *N. ursus*	*Hemigrapsus edwardsii*	*Petrolisthes elongatus*
Matching	11.87%	10.23%	-	-
Contrasting	8.4%	7.78%	-	-
Other species	16.47%	14.94%	27.5%	28.21%

As expected, a greater proportion of the detected non-masking species were eaten compared to *N. ursus* ($G = 192.762$; $p < 0.005$). However, twice the percentage of detected *N. ursus* (both masked and unmasked) were eaten in the presence of non-masking species than with a contrasting background ($G = 4.052$; $p < 0.05$).

14.3.3 Predatory Sequence

Neither the mask, contrasting background, nor species of crab had any effect on the predatory sequence followed by the octopus after initial detection.

14.3.4 Number of Crabs Detected

These results from the differing backgrounds cannot be compared because the number of trials varied for the different conditions. Also,

this category "detected" did not differentiate between crabs which were detected and eaten in the same sequence, and those which had been detected and subsequently ignored one or more times before being finally eaten. Finally, there was no control over what the crabs did before they were detected (e.g., were they perceived because a neighbour(s) moved, or did they move more than their neighbour(s) did?).

14.3.5 Distal Detection

If the three transition frequencies NFR, TP and A were compared separately, the mask had no effect on the pathway followed by a predatory octopus (Table 14.2). However, if NFR and TP were lumped as 'not attacked' (NA), significantly fewer masked crabs were attacked at this stage ($G = 3.942$; $p < 0.05$). Since the difference was barely significant, it is also interesting to note that the lowering of the probability of immediate attack for masked crabs resulted in an increase of the probability of NFR and not TP.

There was no statistical difference in the response to masked and unmasked crabs against a contrasting background. The contrasting background did not change the response to unmasked crabs either. However, significantly more masked crabs were immediately attacked against a contrasting background compared to the matching one ($G = 13.09$; $p < 0.005$).

When *H. edwardsii* and *P. elongatus* were added to the matching background, the octopus still gave the same response to masked and unmasked crabs. However, the presence of these other species resulted in twice the proportion of unmasked crabs ($G = 6.168$; $p < 0.05$) and five times the percentage of masked crabs ($G = 10.556$; $p < 0.01$) being attacked compared to their absence. Visual examination of the data indicated a difference in the octopuses' response to the different crabs, especially between *H. edwardsii* and the others. However, statistical analyses revealed only one difference: omitting the immediate attack data (A), more *H. edwardsii* elicited NFR than *P. elongatus* ($G_{adj} = 11.442$; $p < 0.005$).

14.3.6 Non-oriented Contacts (NOC)

Significantly fewer masked than unmasked crabs were contacted without prior orientation by the octopus with the matching background ($G = 4.95$; $p < 0.05$) (Table 14.3), but there was no significant difference

Table 14.2 Percentage of responses given to crabs after distal detection.

Background	Response	Masked *N. ursus*	Unmasked *N. ursus*	*Hemigrapsus edwardsii*	*Petrolisthes elongatus*
Matching (7 octopuses)	NFR	35.99% (68)	32.35% (55)		
	TP	61.38% (116)	60.59% (103)		
	A	2.65% (5)	7.06% (12)		
	Total	189	170		
Contrasting (5 octopuses)	NFR	25.1% (60)	26.72% (66)		
	TP	65.27% (156)	64.78% (160)		
	A	9.62% (23)	8.5% (21)		
	Total	239	247		
Other species (6 octopuses)	NFR	24.14% (14)	22.86% (16)	32.31% (21)	17.74% (11)
	TP	62.07% (36)	60.0% (42)	49.23% (32)	61.29% (38)
	A	13.79% (8)	17.14% (12)	18.46% (12)	20.97% (13)
	Total	58	70	65	62

Table 14.3 Percentage of crabs contacted without prior orientation by the octopus.

Background	Response	Masked *N. ursus*	Unmasked *N. ursus*	*Hemigrapsus edwardsii*	*Petrolisthes elongatus*
Matching	NOC	18.31% (26)	29.45% (43)		
	OC	81.69% (116)	70.55% (103)		
	Total	142	146		
Contrasting	NOC	6.02% (10)	5.33% (9)		
	OC	93.98% (156)	94.67% (160)		
	Total	166	169		
Other species	NOC	40.98% (25)	27.59% (16)	25.58% (11)	28.30% (15)
	OC	59.02% (36)	72.41% (42)	74.42% (32)	71.70% (38)
	Total	61	58	43	53

between these crabs against a contrasting background. Both masked ($G = 11.4$; $p < 0.005$) and unmasked ($G = 9.414$; $p < 0.005$) crabs were contacted without prior orientation less often against a contrasting background than against a matching one.

In the presence of non-masking crabs, significantly more masked than unmasked crabs were contacted without prior orientation ($G = 11.782$; $p < 0.005$). The presence of these other crabs also resulted in more masked crabs being contacted withour prior orientation compared to the matching ($G = 11.088$, $p < 0.005$) and contrasting conditions ($G = 37.162$; $p < 0.005$) and in significantly more unmasked crabs being contacted without prior orientation compared to the contrasting background ($G = 18.818$; $p < 0.005$).

H. edwardsii and *P. elongatus* were contacted without prior orientation equally often but significantly more masked crabs were contacted without prior orientation compared to the other three crabs ($G = 7.23$; $p < 0.01$).

14.3.7 Response of Crabs to Octopus Contact

Neither the algal mask, a contrasting background, nor the presence of the other crab species had any effect on the proportion of *N. ursus* which moved (Table 14.4).

There was no difference between *H. edwardsii* and *P. elongatus* in their response to contact by the octopus, but the proportion of these non-masking crabs which moved was approximately seven times greater than that of *N. ursus* ($G = 26.266$; $p < 0.005$).

14.3.8 Response of Octopuses to Immobile Crabs

The algal mask and the presence of other crabs species had no effect on the attacks on immobile crabs, and the octopus responded the same way to all four crab types (Table 14.5). Surprisingly, a contrasting background resulted in half the proportion of masked immobile crabs being attacked compared to a matching background ($G = 7.896$; $p < 0.005$), although it made no difference to the octopuses' response to unmasked crabs.

Table 14.4 Response of crabs to contact by an octopus.

Background	Response	Masked *N. ursus*	Unmasked *N. ursus*	*Hemigrapsus edwardsii*	*Petrolisthes elongatus*
Matching	Moved	5.63% (8)	10.96% (16)		
	Not moved	94.37% (134)	89.04% (130)		
	Total	142	146		
Contrasting	Moved	3.01% (5)	7.69% (13)		
	Not moved	96.99% (161)	92.31% (156)		
	Total	166	169		
Other species	Moved	4.92% (3)	3.45% (2)	27.91% (12)	26.42% (14)
	Not moved	95.08% (58)	96.55% (56)	72.09% (31)	73.58% (39)
	Total	61	58	43	53

Table 14.5 The response of octopuses to immobile crabs.

Background	Response	Masked *N. ursus*	Unmasked *N. ursus*	*Hemigrapsus edwardsii*	*Petrolisthes elongatus*
Matching	Attacked	20.89% (28)	14.62% (19)		
	NFR	79.1% (106)	85.38% (111)		
	Total	134	130		
Contrasting	Attacked	9.32% (15)	10.26% (16)		
	NFR	90.68% (146)	89.74% (140)		
	Total	161	156		
Other species	Attacked	13.79% (8)	17.86% (10)	19.35% (6)	10.26% (4)
	NFR	86.21% (50)	82.14% (46)	80.65% (25)	89.74% (35)
	Total	58	56	31	39

14.3.9 Response of Octopuses to Moving Crabs

The small sample sizes obtained for this criterion did not justify a statistical analyses.

14.3.10 Number of Crabs Attacked

As the number and length of trials varied between octopuses and between experimental conditions, the effect of the mask, contrasting background, and type of crab on the total numbers of attacks made cannot be ascertained.

14.3.11 Ability of Octopuses to Hold Attacked Crabs

Examination of the data for individual octopuses revealed that octopus 13 was giving aberrant results. This individual was unable to hold *N. ursus* regardless of the mask or the experimental situation. Octopus 13 was, however, able to hold 30 - 40% of the non-masking crabs. This result may have been an experimental artefact as octopus 13 held and ate all four crab types without difficulty in her home area. If the data for octopus 13 are omitted, over 90% of crabs could be held, irrespective of the mask, background, or type of crab (Table 14.6). As this 10% inability to hold crabs was not observed elsewhere, it too was probably an artefact of the experimental conditions.

14.3.12 Crabs Eaten

Of the octopuses who managed to hold crabs, all individuals, regardless of their species, ate the majority of the non-masking crabs *H. edwardsii* and *P. elongatus* (Table 14.7). From a comparison of the pooled data, there was no difference between the proportion of *H. edwardsii* and *P. elongatus* crabs eaten.

An examination by eye of the *N. ursus* crabs eaten revealed considerable variation attributable to the species of the octopus predator. So the data for each species were analysed separately. In a matching background, *R. australis* rejected significantly more masked ($G = 17.648$; $p < 0.005$) and unmasked ($G = 9.164$; $p < 0.005$) crabs than *O. maorum*. *R. australis* also rejected more masked ($G = 9.164$; $p < 0.005$) than unmasked

Table 14.6 Ability of octopuses to hold attacked crabs.

Background	Response	Masked *N. ursus*		Unmasked *N. ursus*		*Hemigrapsus edwardsii*		*Petrolisthes elongatus*	
Matching	Held	100%	(31)	100%	(28)				
	Not held	0%	(0)	0%	(0)				
	Total		31		28				
Contrasting	Held	93.33%	(28)	94.12%	(32)				
	Not held	6.67%	(2)	5.88%	(2)				
	Total		30		34				
Other species	Held	100%	(17)	90.91%	(20)	92%	(23)	96%	(24)
	Not held	0%	(0)	9.09%	(2)	8%	(2)	4%	(1)
	Total		17		22		25		25

Table 14.7 Crabs eaten by *Octopus maorum* and *Robsonella australis*.

Background	Response	Masked *N. ursus*	Unmasked *N. ursus*	*Hemigrapsus edwardsii*	*Petrolisthes elongatus*
R. australis					
Matching	Eaten	16.67%	28.57%		
	Not eaten	83.33%	71.43%		
	Total	6	7		
Contrasting	Eaten	16.67%	15.38%		
	Not eaten	83.33%	84.62%		
	Total	6	13		
Other species	Eaten	0%	0%	100%	100%
	Not eaten	100%	100%	0%	0%
	Total	1	2	1	3
O. maorum					
Matching	Eaten	100%	95.24%		
	Not eaten	0%	4.76%		
	Total	25	21		
Contrasting	Eaten	90.91%	94.74%		
	Not eaten	9.09%	5.26%		
	Total	22	19		
Other species	Eaten	87.5%	72.22%	95.45%	90.48%
	Not eaten	12.5%	27.78%	4.55%	9.52%
	Total	16	18	22	21

($G = 54.706$; $p < 0.005$) crabs in the contrasting background compared to *O. maorum*. However, in the presence of the non-masking crabs there was no difference between masked and unmasked crabs rejected between the two octopus species. This result may be an anomaly caused by insufficient data.

Analysis of the pooled data for *O. maorum* octopuses revealed no difference attributable to the mask, background, or type of crab. Pooled data for *R. australis* were insufficient to warrant analysis.

14.4 DISCUSSION

This chapter has been concerned with an investigation of the interaction between *N. ursus* and predatory octopuses, with the aim of determining the possible anti-predatory function of the algal mask, its mode of operation and the other behaviours involved in the maintenance of its effect.

14.4.1 Matching Background

Under simulated natural conditions the presence of the algal mask did not affect the predatory sequence shown by either *R. australis* or *O. maorum*. However, it was responsible for significant differences in transition probabilities at two stages along this pathway.

Of the *N. ursus* detected from a distance, significantly fewer masked than unmasked crabs elicited an immediate attack, the same proportion elicited proximal contact, and more masked than unmasked elicited no further response from the octopuses. Together, these results imply that, distally, the mask was confusing the cues which normally trigger an attack, i.e., it was functioning as a primary defence against the octopuses. Primary defences can be transmitted through the visual, tactile or chemical media. The algal mask of *N. ursus* could be procryptic (either eucryptic or special protective resemblance) against both the visual or chemo-tactile senses of the octopus. Alternatively, the mask could be aposematic against the octopuses' chemo-tactile sense (Section I). The other possible primary defence, anachoresis, was prevented by ensuring that the crabs had no hiding places.

In addition to influencing immediate attacks based on distal cues, the presence of the mask resulted in two-thirds the percentage of individuals (18.3%) being contacted without prior orientation compared to unmasked crabs (29.5%). One would not expect the algal mask to have any bearing on the percentage of individuals contacted without prior orientation. Hence, this difference may reflect the fact that these contacts were, in fact, intentional, the octopus being unsure of the stimulus and this seeking further information from proximal cues. If this is true, then fewer masked crabs than unmasked ones were perceived as being possible prey, reinforcing the hypothesis that the mask is a primary defence.

If the mask does function as a primary defence, fewer masked crabs should be initially detected than unmasked crabs. To test for the full effects of the mask as a primary defence, it would be necessary to compare the relative proportions of masked and unmasked crabs which were, and were not, detected. Unfortunately, the design of these experiments did not allow an investigation of the events prior to the actual detection of the crabs. Hence, this aspect has been considered in a separate experiment (Chapter 15).

Once the crabs are physically contacted, an octopus abandons its visual sense and employs instead its tactile and chemical senses which are mediated through the suckers. However, since the octopuses failed to differentiate between masked and unmasked immobile crabs after contact, the mask does not function as a primary defence against proximal tactile, nor chemical detection.

Once the crabs were attacked, the mask did not influence the octopuses' abilities to hold the crabs, so the hypotheses that the mask provides a noxious chemical or tactile stimulus or a mechanical barrier can both be dismissed. Also, the hypothesis that the mask has toxic properties can be abandoned as the octopuses were never observed to display any caution or reluctance to eat masked crabs nor did they ever display any illness subsequent to ingesting the crabs. Considering that the carapace and its attendant algal mask are not actually ingested, this lack of subsequent illness is to be expected. Although only *Halopteris spicigera* was used as masking material in this experiment, casual observations of encounters between octopuses and crabs bearing

masks or other algal species indicated that none of these algal species resulted in chemo-tactile defence, either primary or secondary.

Since the mask has no evident noxious or toxic properties and since *N. ursus* are palatable to the octopuses, aposematism can be dismissed as an hypothetical reason for the effect of the mask on the outcome of distal detection by the octopus. Consequently, procrypsis is implied. To determine whether the algal mask of *N. ursus* functions as eucrypsis or special protective resemblance it is necessary to discuss the results gained using the contrasting background.

14.4.2 Contrasting Background

When *N. ursus* were presented against a contrasting background, the octopuses reacted similarly to both masked and unmasked individuals. Since masked crabs were not perceived as inedible, the mask is probably not functioning as special protective resemblance by enabling the crab to mimic the algae. Three times as many masked crabs were immediately attacked against a contrasting background as against a matching background, suggesting that the mask enables *N. ursus* to blend with its natural algal-covered environment. As the effectiveness of the mask is dependent on the background, the mask functions as eucrypsis not special protective resemblance. De Ruiter (1952) found that Jays attacked sticks after finding stick caterpillars which mimicked those sticks. Consequently, one would expect that, if the mask was special protective resemblance of the algae, the octopuses would 'attack' the algae after capturing *N. ursus*. However, the octopuses were never observed to 'attack' the algae corroborating the hypothesis that the mask is eucryptic. The octopuses would, however, systematically tentacle probe the algae if a masked or unmasked *N. ursus* was captured in the algae.

The octopus exhibited the same response to unmasked crabs regardless of the background, suggesting that crabs lacking the mask are exposed equally as much in the matching as contrasting background. Initially, this finding suggests that, in their natural environment, unmasked *N. ursus* are not as cryptic to octopuses as they are to humans. However, the result may well have been an experimental artefact as, although heterogeneous, the matching background did not provide any bare areas of sand or silt which would be a better 'match' for unmasked *N. ursus*.

Eucrypsis was found to be effective only if the predator was relying on distal cues. Although the signal(s) (or anti-signals; see Moynihan [1975]) can be transmitted via the tactile (water disturbance) or chemical media, the defence was most likely to be visual eucrypsis for two reasons. Firstly, octopuses are reported to rely heavily on their visual sense when hunting prey, especially from a distance (Wells, 1978). The emphasis on the visual sense was also observed in *O. maorum* and *R. australis* as evidenced by the greater amount of alert behaviour exhibited compared to tentacle probe behaviour. Secondly, in both *O. maorum* and *R. australis*, and other octopuses (Chapter 12), distal cues result in a parachute attack on the stimulus. Maldonado (1964) found that there was an indispensable minimum period of illumination below which the parachute leap cannot be computed. If the attacks are based solely on chemical or tactile cues, light would most likely not affect parachute attacks. However, in order to conclude that eucrypsis is definitely achieved through the visual medium alone, it would be necessary to perform an experiment where possible tactile and chemical cues have been controlled (reported in Chapter 15).

Two other points deserve a mention. Although the mask failed to have any large effect, there were significantly fewer accidental contacts of *N. ursus* against a contrasting background. The explanation for this lies in the octopuses' searching behaviour. In the matching, semi-natural conditions, octopuses relied on their tactile forms of searching, tentacle probe and speculative pouncing. Both these methods result in a high number of contacts without prior orientation by the octopus. Conversely, with a contrasting background the animals did not employ their tactile searching methods so there were fewer non-oriented contacts. This effect of differing backgrounds on the mode of searching technique intimates that *N. ursus* are far easier to detect against a contrasting background.

In addition, although the mask did not affect the response of octopuses to crabs which became immobile when contacted, the change of background increased the effectiveness of the mask. The contrasting background resulted in half the proportion of attacks on masked crabs which remained stationary after contact compared to the matching background. However, the contrasting background did not alter the response of octopuses to crabs which were immobile after being contacted. Possibly, the mask is

a special protective resemblance against contact by octopuses, providing the crab remains immobile.

14.4.3 Other Species

The presence of the two non-masking species, *Hemigrapsus edwardsii* and *Petrolisthes elongatus*, provided some interesting results.

(a) The effect of density

In the presence of other species, of those initially detected, one and a half times more crabs were eaten compared to a matching background lacking other crabs. As both backgrounds are in fact matching, the octopus employs the same searching technique in both, so this cannot explain the difference. However, prior to an octopus physically not being able to retain further stored prey, the greater the prey density, the greater the octopuses' propensity to hunt. Hence, twice the density of crabs would result in this increase in hunting activity. Compared to a contrasting background, there was a significant difference in the proportion of crabs eaten of those initially detected: twice as many were eaten in the presence of other crabs. This would be the result of a combination of the searching technique and increased hunting of the octopuses.

This increase in the propensity to hunt with increasing prey density was also apparent in the attacks on crabs after they had been detected from a distance. In the presence of other species, significantly more (twice as many) unmasked crabs were attacked than with the matching and contrasting backgrounds. Also, five times as many masked crabs were attacked compared to the matching background situation. This large difference is attributable to the compounding of the effect of the mask with a matching background and the effect of density in the other species situation.

The presence of other crabs also had a significant effect on the effect of the mask on distal detection. In a matching background devoid of other crabs, the mask was effective in decreasing attacks, while a contrasting background obliterated this effect. The presence of other crabs also nullified the effect of the mask. The only difference between matching and the other species backgrounds was the presence of more crabs. Hence, the density of prey must alter the effectiveness of the mask.

In the presence of the non-masking species there were significantly more contacts without prior orientation by the octopus compared to a contrasting background. There was also a significant difference between masked and unmasked crabs contacted without prior orientation but, contrary to the matching background, significantly more masked than unmasked crabs were attacked. As the same proportion of unmasked *N. ursus* were attacked in the matching background with and without the other species, 'non-oriented' contacts were the result of the searching techniques employed by the octopuses. However, twice as many masked crabs were attacked in the presence of other species compared to without, i.e., the mask was no longer an advantage against a matching background. Two explanations are possible. The presence of the other two species increased the density, causing the masked crabs to move more in an attempt to maintain their normal individual distance. Alternatively, the masked crabs may not have moved as much as the other three crab types and hence got caught in a blanket attack aimed at one or more of these other three crabs who were moving.

(b) The reaction of octopuses to the non-masking species

An examination of the octopuses' reaction to the two non-masking crabs, *H. edwardsii* and *P. elongatus*, provided some interesting results. The predatory sequence by both *O. maorum* and *R. australis* was the same for both *H. edwardsii* and *P. elongatus*, and it was the same as that given to *N. ursus*. Hence, both masked and unmasked *N. ursus* were responded to as 'crab-type' prey. This suggests that the mask does not make any major change to the predatory behaviour of octopuses but instead has a subtle effect by confusing the distal cues these animals receive. However, an examination of the distal detection data revealed that when *N. ursus* and the non-masking crabs were all presented together, there was no statistical difference in the octopuses' response to all four crab types. Thus, under these conditions the differences in the proportion of crabs eventually eaten of those detected was not attributable to distal cues transmitted by these crabs. But this experiment was not designed to highlight the events prior to distal detection (compare to Chapter 15) so the major effect of the mask may have been missed under these experimental conditions.

14.4.4 The Mask and the Inter-individual Distance of *N. ursus*

The effect of increased prey density reducing the effect of the

eucryptic mask of *N. ursus* provides additional support for the hypothesis of Tinbergen *et al.* (1967) that the spacing out of camouflaged species is attributable to predation pressure.

The minimum inter-individual distance maintained during the active period by intertidal *N. ursus* (*ca.* 20 cm) is not as great as one might expect considering that, in the laboratory, octopuses could detect both masked and unmasked *N. ursus* against a matching background at least 78 cm away under dim red light (0.54 foot lamberts intensity). A consideration of the following points may provide an explanation for this discrepancy. The major disadvantage of spacing out is that it significantly lowers the population density and hence restricts the absolute population size. This situation can be overcome by polymorphism where a species or population is composed of two or more variants on the central theme (e.g., the banded snail, *Cepaea nemoralis*, Ford, 1975). As the frequency of one morph in a polymorphic prey species rises, it is eaten disproportionately often by a predator which hunts by 'search image'. Consequently, since the mortality rate of this morph rises, its fitness falls. This phenomenon, called 'apostatic selection' (Clark, 1962), has been demonstrated by Manly *et al.*, (1972) and is responsible for the maintenance of several morphs within a population. *N. ursus* individuals are not inherently polymorphic to any noticeable extent but, like any organism which covers itself with adventitious materials, is polymorphic once these materials are applied. In fact, *N. ursus* is extremely polymorphic; each individual differs from every other and from itself from one point in time to the next by virtue of the fact that these animals continually replenish the mask. This extreme polymorphism probably accounts for their comparatively reduced inter-individual distance for a eucryptic species.

14.4.5 The Mask and Palatability

Kettlewell (1959) believed that there should be a direct relationship between the degree of edibility of a species and the extent of its anti-predatory specialisation. There can be no disputing that masking, as displayed by *N. ursus* at least, is an extremely specialised behaviour. According to Kettlewell's hypothesis, *N. ursus* should be extremely palatable to predators. However, there was twice the proportion of non-masking crabs eaten, of those initially detected, compared to *N. ursus*. There are several possible explanations for this. Perhaps non-masking crabs

are more palatable, and Kettlewell was mistaken. Alternatively, the non-masking species are easier to catch than *N. ursus*. Finally, perhaps neither *O. maorum* nor *R. australis* are in fact feral predators of *N. ursus* so the non-masking species were more familiar to these predators.

An examination of the proportions of crabs eaten, of those actually attacked and held, reveals that for *O. maorum* there was no difference between all four crab species. This implies that *N. ursus* were no less palatable to *O. maorum* than non-masking crabs, and supports Boyle & Knobloch (1981) who studied the food selection of the octopus *Eledone cirrhosa*. They found that the masking crab *Hyas araneus* was no less preferred than the non-masking species *Cancer pagurus*, *Corystes cassivelaunus*, and *Pagurus bernhardus*. However, these four species were less preferred than *Carcinus maenas* who, in turn, was less preferred than *Macropipus holsatus*. On the contrary, *R. australis* ate fewer *N. ursus* than, but the same proportion of *Hemigrapsus edwardsii* and *Petrolisthes elongatus* as, *O. maorum* regardless of the experimental condition. Since *H. edwardsii* and *P. elongatus* were matched for size with *N. ursus*, this anomaly cannot be accounted for by the size of the crabs. The cautious behaviour exhibited by both *R. australis* specimens may provide a clue to their tendency to reject these animals. In many predators, a prey species with which the predator has successfully fed, becomes increasingly acceptable (Curio, 1976). Octopuses are such predators and *N. ursus* may have been unfamiliar to these particular individuals. This result would then be attributable to the small sample size. Alternatively, *R. australis* as a species may not prey on *N. ursus* in the wild. As *R. australis* were difficult to obtain, I could not determine if this was the case. Consequently, the occasional *R. australis* individuals obtained were not used as predators in the ensuing experiment (Chapter 15).

14.4.6 Anti-predatory Behaviour of Crabs

An investigation of the crab's response to contact by octopuses revealed that there was no difference between the proportion of masked and unmasked *N. ursus* who remained immobile, regardless of the experimental situation. Thus, the mask has no apparent effect on immobility. As immobility occurred after the octopus initiated a prey-catching attempt, it was a secondary defence. *H. edwardsii* and *P. elongatus*, on the other hand, showed a significant difference in behaviour compared to *N. ursus*:

seven times as many non-masking crabs moved when contacted, implying that immobility in response to contact is a behaviour of especial importance to cryptic animals. Observation of those crabs which moved showed that they tended to replace immobility with retaliatory or flight behaviours.

An examination of the reaction of both *O. maorum* and *R. australis* to contact with immobile crabs shows that when all four crabs were present, the type of crab had no effect on the effect of immobility: 80 - 90% of immobile crabs elicit no further response. The fact that a substantially lower proportion of non-masking crabs became immobile after contact meant that a lower proportion of these crabs were going to be ignored compared to *N. ursus*. Thus, the difference in the percentage of crabs eaten of those initially detected between masking and non-masking species was largely attributable to differences in the behaviour of those species, not their palatability.

14.4.7 Evaluation of Methodology

It is important to remember that laboratory experiments can provide evidence about beneficial consequences only in the circumstances in which they were conducted. This study had several drawbacks apart from the usual ones associated with laboratory experiments. The octopuses were not restricted to using only one type of sense organ, hence it was impossible to determine the medium through which the eucryptic mask was effective. Secondly, the predators were not restrained from using tentacle probes and speculative pounces, which both increased the chance of an animal being detected by accident. The mode of attack was also uncontrolled and 'blanket' type attacks resulted in crabs being captured by accident. Finally, as a result of using appetitive octopuses, analysis was rendered more difficult than usual as individual trials were of varying lengths and, consequently, there were also varying numbers of trials/day.

The analyses of the data reported here suggest that the most fruitful areas to research further are the events prior to detection of *N. ursus* by the octopus.

- - -

To summarise, *N. ursus* are treated as 'crab' prey, and the mask does not change the predatory sequence by *O. maorum* and *R. australis* However, the experiments reported above have shown that, once a stimulus has been detected, the mask has a subtle effect, impairing the octopuses' predatory success by confusing the orientation or triggering of attack based on distal cues. In all probability, the mask may also frequently be a primary defence, effective in preventing the actual detection of the crabs. As the present experiment did not allow this to be determined, it will be necessary to investigate this more fully under a different set of experimental conditions (Chapter 15).

SECTION II

CHAPTER 15

THE MASK AS VISUAL CRYPSIS

15.1 INTRODUCTION

Although marginally statistically significant, the difference obtained between the attacks on crabs with and without the mask was small (Chapter 14) in view of the time and energy *Notomithrax ursus* expends masking (Chapters 1 and 5). The mask may not, in fact, be an anti-predator adaptation, but the evidence presented in Section I makes this explanation unlikely. A small advantage is consistent with the traditional Darwinian view (e.g., Holling, 1965) that evolution on a grand scale is merely the compounding of the effects of small-scale evolution resulting from slight advantages in survival. However, the advantage conferred by the mask may be much greater in the field but the uncontrolled variables present in the observational context (Chapter 14) prevented the full exposure of this advantage.

While suitable for determining which major function the mask was likely to fulfil, the experiments presented in Chapter 14 were not suitable for the exact delineation of the mode of effect of any particular function. Assuming, as do many authors, that the mask is visual eucrypsis, then as *N. ursus* are nocturnally active, it was important to test if illumination plays a role in the effect of the mask. As immobility is generally considered very important for the maintenance of crypsis (Edmunds, 1974), the effect of movement by *N. ursus* also needed to be investigated. Finally, visual eucrypsis can be achieved by means of three distinct mechanisms: homochromy, disruption of body outline, and changing the effects of incident light (i.e., shadows, Cott, 1940; Friedmann, 1944; Edmunds, 1974) and it was of interest to determine which of these mechanisms achieved eucrypsis.

The aim of this chapter then, was to control the extraneous variables encountered during the observational study (Chapter 14) to determine if the advantage conferred by the mask is indeed as small as previously found.

It was not only important that the mask was presented so as to maximise the cryptic effect, it was also important that the octopus was operating to the best of its ability. Consequently, the following experiment was designed to cater for the special requirements of octopuses, discerned in Chapter 12. Octopuses are trained readily (Boycott, 1965) and Sutherland *et al.* (1963) established that the simultaneous presentation of stimuli is a more effective training method for *Octopus* if these animals have a difficult discrimination task. When presented against a matching background, masked crabs should be very difficult to discriminate: hence, a masked and an unmasked crab were presented simultaneously. Pre-training, commonly employed as part of discrimination training with octopuses (Sutherland, 1958, 1961; Rhodes, 1963; Messenger *et al.*, 1973) was used to train the octopuses where to locate the crabs and to ensure that upon location of a 'prey' they made an immediate parachute attack, retrieved their captive, and returned to their home area. Pre-training octopuses to this procedure ensured that attacks were made on distal cues only; that octopuses did not have to be disturbed to chase them home after completion of a trial, and that the octopuses were familiar both with the experimental tray and with the mode of presenting crabs, as neither of these factors would have been encountered by feral octopuses. Since octopuses will attack crabs dangled on a string or rod (Wells, 1962, 1978; Rhodes, 1963; Messenger, 1968; Walker *et al.*, 1970), *N. ursus* were presented on easily broken transparent thread.

With the traditional experimental group, control group, statistical analysis method of doing research, individual variations (often quite large) are masked in the group average. An alternative approach to the group statistical design is the single-case experimental design, a method which is becoming increasingly popular in psychiatric research (Barlow *et al.*, 1973). This involves testing the effect of a variable(s) by subjecting one individual to a large number of replicate trials/variable. Although single-case designs provide the researcher with information on the effects of the variable for subjects with the same characteristicts, their results also may not be applicable to <u>all</u> subjects. The answer to this problem is to apply the variable to subjects with different background histories, an approach which Sidman (1960) refers to as systematic replication. Differences in result can then be ascribed to specific subject characteristics, such as species of octopuses, its size or depth it lived at etc. Hence, single-case design experiments highlight individual

differences rather than averaging them out. Since octopuses exhibit large, individual differences (Chapters 12 and 14), systematic replication of the single-case design was used for this experiment.

Many published selection experiments concerning camouflage have not had sample sizes large enough to analyse statistically. To obtain a comparison with these results, and to provide an additional parameter for the evaluation of my experiments, I also considered the data using Dice's (1947) selection index:

$$\text{Selection index} = \frac{a - \frac{1}{2}(a + b)}{\frac{1}{2}(a + b)} = \frac{a - b}{a + b}$$

where a and b, respectively, are the numbers taken of the two types A and B, and $\frac{1}{2}(a + b)$ is the expected value of a. The selection index may vary between +1.0 and -1.0, being 0.0 when there is an absence of selective effect. The significance of the deviation of the selection index from 0.0 can be tested by the usual Chi-square formula for a 1:1 ratio:

$$\text{Chi-square of selection index} = \frac{(a - b)^2}{a + b} .$$

As a result of the foregoing requirements, an experiment was designed so that *O. maorum*, pre-trained to make immediate attacks, were exposed to masked and unmasked *N. ursus* which were both tethered and moving equally against a background composed of the same alga as, and hence matching, the mask. The variables of prey movement and illumination were altered to enable a demonstration that the mask was affecting the visual perception of distal cues by *O. maorum*. The method used in this work conformed to the standard procedures for conducting discrimination experiments using octopuses, as outlined by Wells (1978) and Rhodes (1963). However, it is important to note that this experiment was aimed at testing the octopuses' ability to detect masked and unmasked crabs, not choose between them.

15.2 MATERIALS AND METHODS

15.2.1 Experimental Apparatus

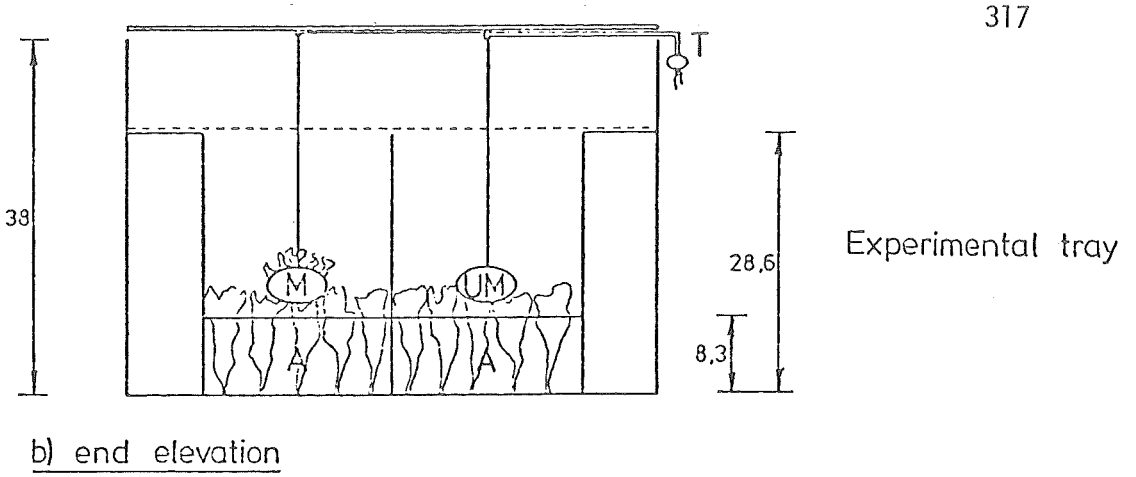
These experiments were conducted in the experimental aquarium

previously described in Chapter 13.2. There were, however, substantial changes to the removable tray. To prevent *O. maorum* from simultaneously blanket-attacking both sides of the tray, it was divided in half, widthwise, by a perpendicular division. The octopuses could still view either half of the tray equally well (Fig. 15.1a). A matching background was provided by filling both sides of the tray equally with living *Halopteris spicigera* to a depth of 12 cm. Removal of the algal clumps was prevented by affixing their holdfasts to the tray bottom with 'Bostik Quickset epoxy resin' (non-contaminating). To ensure that neither masked nor unmasked crabs were unnaturally highlighted the black interior surfaces of the tray were daubed with randomly placed, irregular shaped patches of paint of a shade approximating that of *H. spicigera*.

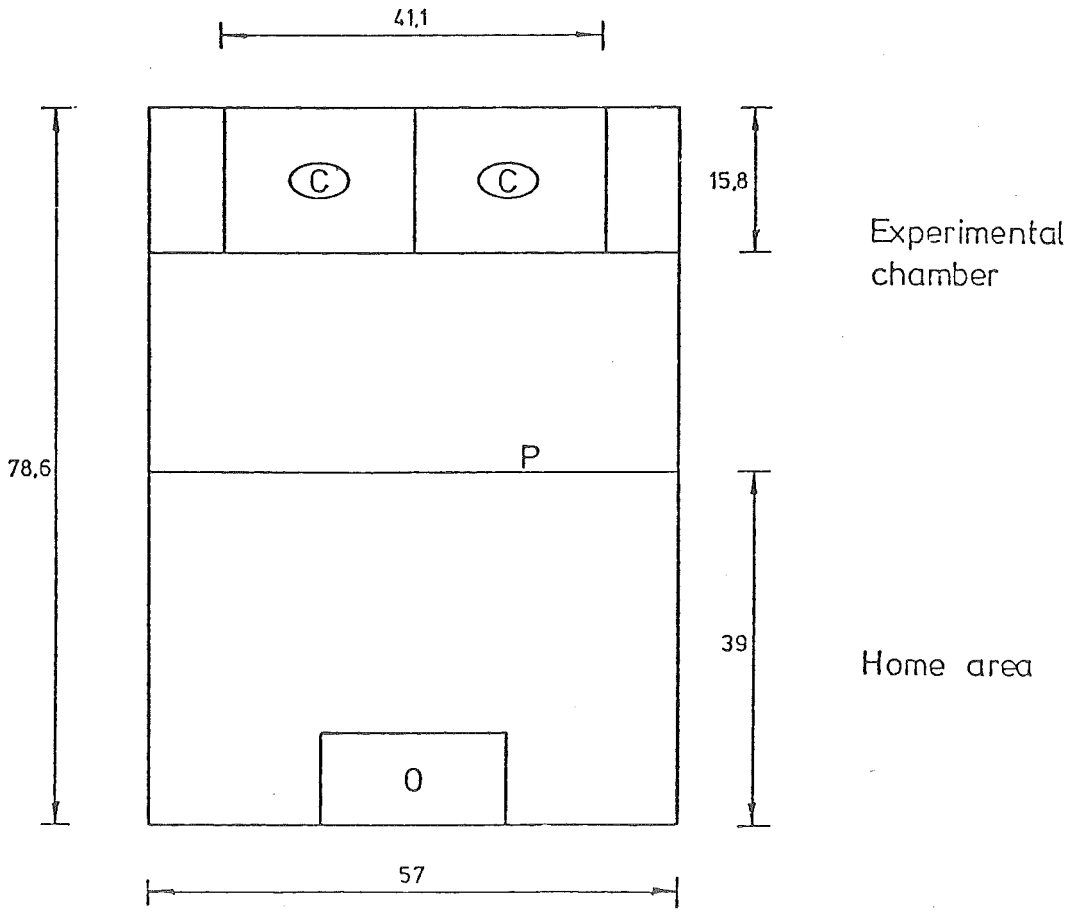
N. ursus used in this experiment ranged in carapace length from 14.4 to 34.6 mm and were suspended, one on either side of the tray, by fine transparent thread. This method ensured that *N. ursus* were always presented in identical positions on either side of the tray, that they moved equally and that they could not actively avoid capture. The crabs could be simply attached by passing one end round the carapace, between the first and second pairs of legs, and knotting it. Also, the octopuses were able to break the thread and hence take their captives home to eat.

The mode of presenting the suspended crabs is shown in Fig. 15.1b. A sturdy brass rod was positioned over the longitudinal axis of the tray. Rings were welded along one side of this rod to the mid-point of the first half of the tray, and along the opposite side to the mid-point of the second half of the tray. A clip hook and weight were attached to one end of two lengths of transparent 0.018 fishing gut (9 kg breaking strain). One piece of gut was then threaded through the rings on each side of the rod, so that the free ends came out on the experimenter's side of the tank. These ends were knotted together through a third weight so that the weights at the other end hung 4 cm down from the brass rod. Crabs were each tied with the free ends of equal lengths of the fine thread which had a brass ring attached to one end, and these rings could be slipped easily over the hooks on the overhead gut, ensuring that the crabs could be presented with the minimum disturbance to the octopuses.

Octopuses respond best to vertical movements of stimuli, especially at a speed of 2 - 4 movements/sec (Chapter 12). Crabs could be moved in this



b) end elevation



a) plan diagram

Fig. 15.1 Experimental aquarium (← 57 → cm).

(a) Plan diagram of aquarium; C, crab, O, octopus home; P, movable black partition.

(b) End elevation of experimental tray (i.e., view available to octopus once the partition was raised; A, the alga *Halopteris spicigera*; M, masked *Notomithrax ursus*; T, transparent thread; UM, unmasked *N. ursus*. Broken line shows water level.

manner by pulling the 'knot' down 4 cm, so that the counterweights touched the rod, and releasing it again, two times/sec. With this system it was possible to move the crabs manually or by mechanical means. Little practice was required to achieve a steady rate of two perpendicular movements/sec over a 4 cm distance.

Three female and two male *O. maorum* (300 - 599 g) (Nos. 22-26) were used as the predators in this experiment. The experimental octopuses were caught, transported, quarantined, and acclimatised to the experimental aquaria in the same manner as described in Chapter 13.

Pre-training was achieved in stages, by first exposing the octopus to feeding crab on the transparent thread, in the home area, then in the experimental chamber and finally over the algae in the tray. *Hemigrapsus crenulatus* were used as feeding crabs as they represented a totally different 'crab-shape' than either masked or unmasked *N. ursus*. Throughout training, only one crab was presented at each trial and the side on which it was presented was randomised by tossing a coin. Sutherland and Muntz (1959) found that in a simultaneous training situation, learning of a task is virtually complete after only ten pre-training trials on the positive shape. However, pre-training was continued until learning was affirmed by an octopus consistently making an immediate parachute attack, retrieving the crab and returning it to its home.

To negate the possibility that during experimental trials octopuses could see only one of the two crabs, the brick home was situated on the mid-line of the home area and no trials occurred unless the octopus was either in or on its home or on the floor immediately in front of its home.

15.2.2 Experimental Procedures

(a) Standard procedure

During experimental trials, two *N. ursus* of approximately equal carapace length were suspended from the rod, one on either side of the partition so that their bodies just touched the algae (Fig. 15.1b). As in previous experiments, one crab had its mask intact, while the mask of the other had been removed with forceps, leaving the body hairs intact. When the octopus was exhibiting appetitive behaviour in or on its home, the partition separating it from the experimental tray was raised and the

crabs were manually "jiggled" up and down two times/sec. The partition was lowered when the octopus had made a capture and returned to the home area or after 5 min elapsed without an attack being made.

Trials were repeated, with new crabs, each day until the octopus no longer entered the experimental chamber; hence, the number of trials/day was variable. However, each octopus was tested on successive days until it completed 50 experimental trials.

Randomly positioned control trials were used to ensure that the octopuses were reacting to the crabs and not to extraneous cues such as the raising of the partition. Control trials were identical to the experimental ones, except that no crabs were presented on the end of the thread. The side on which masked crabs were presented was randomised and masked crabs were never presented on the same side for more than five times in succession. In the eventuality that some of my movements were apparent to the octopuses, I was careful to keep crabs hidden from them and to make exactly the same movements over both sides of the tray, whether or not crabs were being presented.

Experiment 1: Effect of the mask

Nineteen trials, using only one octopus (No. 22) were conducted at the light intensity of 0.54 foot lamberts at 16.6 cm depth. As the difference in attacks on masked and unmasked crabs was not large, the experiment was modified to test for two variables which may have affected the result.

Experiment 2: Effect of illumination on the effectiveness of the mask

The light intensity used in Chapter 14, and again in experiment 1 of this chapter, was much higher than the conditions in the field at night, even at full moon (see Table 13.1). Illumination needed to be this high to enable the experimenter to observe all the fine details of the *N. ursus*/ octopus interactions. However, under the present experimental conditions, it was only necessary to observe whether an attack was made and to ensure that the attack was made on distal cues (i.e., a parachute attack). Accordingly, the light intensity could be lowered until the experimenter could only discriminate the shape of an octopus as it parachute attacked one or other side of the tray. In my case, this intensity was 0.11 foot

lamberts at 16.6 cm. This reduced light intensity was achieved by covering the red fluorescent tube with four layers of 2 mm^2 plastic mesh.

The same procedure was followed as described for experiment 1. However, as the octopus was showing a marked differential discrimination, 50 trials were run with octopus 22. To ensure that octopus 22 was not an aberrant example of its species, the experiment was repeated with four further octopuses, each for 50 trials.

Experiment 3: Effect of immobility on the effectiveness of the mask

Observations and preliminary experiments in Chapter 2 confirmed the work of other authors that octopuses require movement to elicit attacks based on distal cues. Observations on *N. ursus* in Section I, Chapter 8, and Section II, Chapter 14, indicated that these *N. ursus* did not move much, especially in the proximity of predators. Accordingly, experiment 2 was repeated with stationary crabs to see if immobility enhanced the effect of the mask against an *O. maorum* predator (No. 22). To ensure absolute immobility, the crabs used were killed in fresh water 2 - 3 h prior to use.

Five preliminary trials revealed that the octopus was parachuting the area above the crabs and finding them by working down the threads. A further ten preliminary trials without string revealed that the octopus was not discriminating between masked and unmasked. However, it was also possible that the octopus may have been expecting crabs to be on both sides of the tray. To exclude the possibility of the octopus making chance attacks, the experiment was modified so that only one crab was presented/trial. Consequently, there were five possible combinations: -/M, M/-, -/UM, UM/- and -/-, the latter being a control trial. Twenty-four trials were conducted with octopus 22, and the order of the five combinations was randomised.

(b) Analysis

The octopus was said to have discriminated a crab only when it had made a parachute attack AND this attack had to have been made from its home, a distance of *ca.* 70 cm away. These attacks were counted regardless of the octopus's success, or even lack of an attempt, at retrieving its capture.

The sample size obtained from each octopus, in all three experiments was sufficient to test the significance of the data for each individual using a G_{adj}-test. The results for the five octopuses in experiment 2 were tested for homogeneity with a G_H-test and then combined and tested for significance using the G-test. As the formula for the calculation of the selection index applies only to a situation in which the numbers of two types of prey are equal when selection occurs, it could not be applied to experiment 3.

15.3 RESULTS

Experiment 1: The effect of the mask

After 19 trials with octopus 22 under a light intensity of 0.54 foot lamberts, there was no detectable difference in the numbers of masked and unmasked crabs attacked first (12 masked : 7 unmasked).

Experiment 2: The effect of illumination on the effectiveness of the mask

A G-test analysis comparing the attacks on masked and unmasked crabs at the two light intensities showed that light intensity was an important variable for the effect of the algal mask (G_{adj} = 15.078, $p < 0.005$) (see Table 15.1).

A further four octopuses (numbers 23, 24, 25 and 26) tested at this lowered illumination, for 50 trials each, also attacked significantly more unmasked first than masked (see Table 15.3). As the results obtained for all five octopuses were not significantly different (G_H = 1.326, n.s.), the data were pooled and the mask was found to have a highly significant effect in preventing its possessors from being attacked (G = 141.9192, $p < 0.005$) (see Table 15.2).

The data for these five octopuses were also converted to Dice's (1947) selection index and all indices so derived were highly significant (see Table 15.2).

Analysis, by a Mann-Whitney U-test, transformed to approximate the t-distribution, provided no evidence that, for any of the five octopuses,

Table 15.1 Number of masked and unmasked *Notomithrax ursus* attacked by a single *Octopus maorum* under two light intensities.

N. ursus attacked	Light intensity (foot lamberts) at 16.6 cm depth	
	0.54	0.11
Masked	12	6
Unmasked	7	44

Table 15.2 Number of masked and unmasked *Notomithrax ursus* attacked by *Octopus maorum* under dim red light (intensity: 0.11 foot lamberts at 16.6 cm depth).

Octopus maorum			*Notomithrax ursus* attacked			Statistics ($p < 0.005$)		
No.	Sex	Weight (g)	Total	Masked	Unmasked	G	Selection Index	Chi-square Selection Index
22	M	650	50	6	44	30.676	-0.76	28.88
23	F	495	50	8	42	23.726	-0.68	23.12
24	F	400	50	6	44	30.676	-0.76	28.88
25	F	300	48	9	39	18.780	-0.63	18.75
26	M	650	50	6	44	30.676	-0.76	28.88
Total			213	35	248	141.919	-0.718	127.76

Table 15.3 Octopuses' latency to attack those crabs of a pair which were attacked first ($p > 0.05$).

Octopus maorum (No.)	Median latency to attack		Mean latency to attack		t_s
	Masked	Unmasked	Masked	Unmasked	
22	0.75	1.0	1.41	1.05	0.14
23	1.0	0.75	1.34	1.27	0.17
24	0.75	1.0	1.54	0.99	0.64
25	0.5	0.625	0.72	0.97	0.43
26	5.0	0.5	0.58	0.83	1.35

the algal mask affected latency to attack those crabs of a pair which were taken first (see Table 15.3).

Although the algal mask had no effect on their latency to attack, the octopuses exhibited a marked difference in their reaction to masked and unmasked crabs. When an unmasked crab was presented on the same side of the tray, say A, for several consecutive trials, then that octopus would rapidly attack side A immediately the partition was raised in the following trial. However, when an unmasked crab was then presented on side B the octopus displayed 'hesitant' behaviour, orienting first to side A then to side B, continually bobbing its 'head'. This alternation would continue until suddenly the octopus would attack the unmasked crab. This 'hesitancy' was exhibited by all five octopuses, but only to the unmasked crabs. On the 35 occasions when masked crabs were attacked first, no hesitancy was observed. A further interesting observation was that in 2 of the 35 trials where masked crabs were attacked first, the octopus had initially been moving towards the unmasked crab, but had stopped part-way down the tank and switched direction to attack the masked crab. The reverse situation was never observed.

Evaluation of the method used in experiment 2

Only 261 trials had to be conducted to achieve the 248 trials in which the crabs were attacked singly. In 8 of the 12 discounted trials, the octopus attacked masked and unmasked crabs simultaneously (one by octopus 22, six by octopus 23, and one by octopus 24). Data from these trials were discarded. A further three trials were abandoned as the octopus did not make an attack directly from its home; and another was discounted as, although showing appetitive behaviour, the octopus did not enter the experimental area.

Selection biases were not apparent for size, sex or order of presentation of the crabs and there was no evidence suggesting the octopuses had learned that two crabs would be presented on each trial. Control trials demonstrated that the octopuses were reacting to the presence of the crabs rather than to extraneous cues.

In 25 of the 248 accepted trials, a second crab was attacked, always within 1 min of the first attack. Statistical analysis showed

that the mask made no difference to the order of attack (G_{adj} = 2.6054, n.s.) nor to the latency of attack within each pair ($Us_{[17,8]}$ = 85, n.s.). Neither were there any apparent differences in the order or latency of attack within each pair which were attributable to the size of the crabs.

Experiment 3: The effect of immobility on the effectiveness of the mask

The attempt to determine the effect of immobility of the crabs on the effect of the mask in lowering the probability of attack had to be abandoned after 24 trials (4 controls and 20 experimentals) as in all but two trials (one masked and one unmasked) the octopus would not make parachute attacks direct from its home. The octopus showed more interest in unmasked crabs: five of the six crabs attacked were unmasked. However, the octopus had searched the other side as well, before making a slow attack on these crabs. This searching of the sides was not due to any side preference as one side was searched twice, the other three times. The single masked crab attacked was approached very slowly, but the octopus did not search the other side.

15.4 DISCUSSION

15.4.1 The Effect of Illumination

The experimental results provide evidence that the mask protects *N. ursus* from attack by predatory octopuses. However, an especially important finding that warrants emphasis is that the effectiveness of the mask depends on ambient light intensity. Under dim red light of 0.54 foot lamberts intensity the experimenter had considerable difficulty in perceiving masked crabs, but could detect unmasked crabs, amongst the *Halopteris spicigera*. In contrast, the *O. maorum* displayed no hesitancy in attacking either type of crab, nor was there any evidence of differential predation on masked and unmasked individuals. Conversely, at a reduced intensity of 0.11 foot lamberts, where the experimenter could see only shadows and had trouble detecting even unmasked crabs, the octopus attacked significantly more unmasked than masked crabs. This evident inability to detect masked crabs was further supported by the octopuses' behaviour of vacillating between looking at the side an unmasked crab had been captured in the prior trial, and its current side.

This dependence of the mask for its effect on the light intensity is a reflection of the visual accuity of this nocturnal predator. Although studies have previously been conducted on the ability of octopuses to discriminate in dim light (see Wells, 1978), there appears to be only one other reference to the effect of dim light on octopus predatory behaviour. Taylor & Chen (1969) observed the ability of *O. bimaculatus* to hunt scorpionfish (*Scorpaena guttata* Girard) in the light (intensity not mentioned but daylight implied) and complete darkness. These authors found no evidence of predatory activity in darkness after 30 and 90 minutes respectively, which is not surprising considering that octopuses in the field would rarely encounter absolute darkness.

My experiment demonstrates that the discrimination abilities of *O. maorum* decrease with decreasing light intensity. *N. ursus* is nocturnal and photonegative, not emerging until it is fully dark and seeking cover if it is suddenly exposed to light. The results of this experiment support the hypothesis that visually hunting predators, such as *Octopus*, have been important selection pressures favouring these activity patterns.

Dice (1947), using deer-mice (*Peromyscus maniculatus*) as prey and the barn owl (*Tyto alba pratincola*) and the long-eared owl (*Asio wilsonianus*) as predators, considered the possible dependence of protective adaptations on light intensity. In an elegant laboratory experiment, Dice restricted the owls to visually hunting mice (of different pelage colours which matched or contrasted with the background soil) by the construction of stick 'jungles' to distort the auditory cues which owls use to hunt prey in the dark. Dice found that selection by the barn owl appeared to be operative over 13 light intensities from just below an illumination at which the mice would be inactive due to the light being bright, down to the lowest intensity at which the owl could probably see its prey. The evidence from the long-eared owl was less conclusive but also indicated that selection for the more conspicuous mice occurred over a considerable range of illuminations. More importantly, he found that within this range of intensities there was possibly an optimum intensity (or range of intensities) at which the selection of deer-mice by owls may be more intense. This indication, combined with his (1945) finding that, with decreasing illumination, owls

have increasing difficulty in finding dead prey, led Dice to assume "that selection should be most discriminating at those light intensities where the predator is just barely able to see his prey". The results reported here, from the experiments with *N. ursus* and *O. maorum*, corroborate Dice's hypothesis and suggest that this is a phenomenon of general importance when considering the evolution of eucrypsis in animals.

The fact that illumination affects the octopus's discrimination of masked *N. ursus* lends support to the hypothesis that the algal mask acts as visual eucrypsis against *O. maorum*. Lowering light intensity changes the visual cues to the octopus but not chemical and vibratory ones which the predator may use in prey detection. At very low light intensities, the visual capabilities of the octopus may be strained and a threshold may be reached below which the octopus switches partially, or totally, to another sensory modality such as use of water-borne vibrations for prey location. However, it is unlikely that amongst such relatively large quantities of algae, there would be any detectable differences in water disturbance attributable to the presence/absence of the mask on these crabs. In addition, octopuses were shown (Chapter 12) to react to movement outside the glass viewing panel, but not the opaque sections of their tank, intimating that they were using visual not vibratory cues. Finally, since the experimental octopuses displayed behaviours associated with visual attacks (Chapter 12) at both light intensities, it can be assumed that the algal mask acted as visual eucrypsis.

15.4.2 Latency to Attack

The fact that in masked/unmasked paired presentations unmasked crabs were attacked first, indicated that masked crabs are more difficult to detect. Consequently, one would predict that the latency to attack masked crabs will be greater than that to attack unmasked *N. ursus*. However, under the existing laboratory conditions, there was no evidence that the octopuses were slower in attacking the few masked crabs which were attacked than they were in attacking the unmasked ones. The lack of hesitancy displayed in actually attacking the few masked crabs who were parachuted suggests that these particular crabs were, for some reason, very conspicuous when detected (e.g., may have moved by themselves). Alternatively, this may be a reflection of the fact that the octopuses were trained to expect food in that area and having detected a cue which may be

food, they attacked immediately. In the wild, octopuses may have to take a much longer time to scrutinise the area surrounding a masked *N. ursus* before the crab is 'recognised' as prey. That the masked crabs are generally more difficult to detect is reinforced by three facts. Firstly, other workers (see Wells, 1978 for references) have demonstrated that an increase in presentation of a stimulus to octopuses results in a decreasing delay in attacking that object and in an increase in the probability of attacking a variety of other moving objects that were at first rarely or never attacked. However, with increasing presentation of masked and unmasked crabs there was not an increase in the number of masked crabs attacked, demonstrating that these crabs could not be detected. Secondly, when unmasked crabs had been presented and attacked on side A for two or more consecutive trials and were then presented on side B, the octopus would initially orient to side A, and occasionally start to move towards this side. However, they would quickly stop and then orient to side B. The octopus would then vacillate up to five more times before attacking the unmasked crab. So, although expecting a crab on side A, these octopuses failed to detect the masked crabs. Finally, the ability to detect masked crabs seemed dependent on the octopus-crab distance as in several trials, when the octopus was moving from its home directly to an unmasked crab, it suddenly stopped, switched direction and made an attack on the masked crabs. (These trials were counted as invalid as the octopus did not make a direct attack on either crab.)

15.4.3 Selective Effect

To provide a comparison with the results of this selection experiment with those of other authors, many of whom do not provide enough data to justify statistical analysis, the results were considered in terms of Dice's (1947) 'selection index'. As Dice's selection index concerns survival only, it is, therefore, a very different statistic from the selection co-efficient which, in population genetics, concerns differential reproduction (Wilson & Bossert, 1971). In this experiment, as with those of Dice and the majority of selection experiments, the genotypes of the animals tested were unknown and the selection co-efficients could not be calculated. Although not allowing a direct prediction of fitness, the use of the selection index is not meaningless as, to be represented in future generations, a gene must first survive the rigours

of the present generation. As the majority of *N. ursus* (especially the males) used in this experiment were pre-reproductive animals, it is safe to assume that those individuals which survived would be able to reproduce. Consequently, a determination of the selection index should provide some indication of the 'fitness' of the trait in question, in this case the algal mask.

The selection indices obtained from the five individual *O. maorum* constrained to hunt by visual cues alone, ranged from 0.63 to 0.76. In the field, given that an *O. maorum* is in the vicinity, this range of selection indices may be considerably higher as illumination at night is, at very best, much lower. Also, *N. ursus* remain motionless when approached and the octopus may be hunting in a much larger area. Also, the octopus has a much wider range of prey avaiable in the field. During this experiment the octopus was, in effect, differentially reinforced for attacking only one species of these possible prey, resulting in an increase in predation pressure on that prey.

Table 15.4 presents selection indices obtained, or calculated, from other selection experiments which had an adequate sample size. Although these other experiments concerned the efficacy of concealing colouration rather than adventitious application, the principle is the same in both instances. In each of these experiments, in which the predator was evidently using sight, the cryptic individuals enjoyed more than a 20% advantage over the conspicuous individuals in escaping capture. Such high selection indices make the evolution of 'protective colourations', including adventitious use, readily understandable.

15.4.4 The Effect of Stabilising Selection

Johnson (1976) held that -

> "when we observe a well-perfected development of an advantage-giving attribute that exists for only a short period of the individual's life, we may conclude that rather high s (selection co-efficient) values have operated to generate the adaptive expression".

Assuming that a selection index provides a good estimate of the value of the corresponding selection co-efficient, then selection will be intense for the masking behaviour of *N. ursus*. This high selection co-efficient

Table 15.4 A comparison of the selection indices obtained by various authors investigating the efficacy of cryptic colouration.

Author	Prey Species	Prey Morph	Predator	Selection Index	Chi-square	Derived by
Sumner, 1934	*Gambusia patruelis*	Skin colour	Galapagos Penguin	0.351	6.661	Dice, 1947
Sumner, 1935a	*Gambusia patruelis*	Skin colour	Night heron	0.229	18.978	Dice, 1947
Sumner, 1935b	*Gambusia patruelis*	Skin colour	Sunfish	0.355	30.894	Dice, 1947
Isley, 1938	Acridians	Exoskeleton colour	Birds	0.378	83.816	Dice, 1947
Dice, 1947	*Peromyscus*	Pelage colour	Barn Owl	0.29	16.333	Dice, 1947
Kettlewell, 1958	*Biston betularia*	Exoskeleton colour	Birds	0.726	100.29	Pack (this study)
Kaufman, 1973	*Mus musculus*	Pelage colour	Shrike	0.652	9.8	Kaufman, 1973
Kaufman, 1973	*Mus musculus*	Pelage colour	Shrike	0.625	6.2	Kaufman, 1973
Pack (this study)	*Notomithrax ursus*	Adventitious algal mask	Octopus	0.718	127.76	Pack (this study)

in turn provides a solution for the dilemma (discussed in Section I) of why *N. ursus* should invest in such an energy expending behaviour as masking when it is only exposed to octopuses for such a short time, by virtue of its anachoretic and crevice gripping behaviours.

15.4.5 Applicability of this Experiment to the Field Conditions

As selection occurs in the field, it is important to relate the laboratory conditions to the situation of *N. ursus* in the field.

The criticism that the light intensity in the laboratory was higher than that found during darkness in the field is negated by the fact that, as the mask was effective at the lower of the two laboratory intensities, it follows that the mask will be even more effective in the field where the illumination is even lower than 0.11 foot lamberts.

Since octopuses attacked the crabs directly and not the thread above them, this thread was not influencing their discrimination of the crabs even if these predators could detect it.

Filling the experimental tray with abundant algae of only one species (*Halopteris spicigera*) probably reproduced to a considerable extent the conditions in nature. In the intertidal region where *N. ursus* were collected, the environment consisted of large mono-species patches of algae, the most abundant being *Corallina* sp. and *H. spicigera*. Crabs were often found in these algal patches and at night were observed moving among them (Chapter 7). The predator, however, was not inhibited by the algae and could catch the crabs readily when the light intensity was sufficiently high for it to detect its prey.

A major criticism that can be levelled against experiments of this type is that the character difference obtained is unnatural and/or causes associated physiological or behavioural changes to its possessor. As explained in the methods, unmasked crabs are found in the natural situation after they have moulted and there are no apparent physiological differences caused by removal of the algal mask. Any possible differences in mobility were negated by ensuring that both crabs moved simultaneously and for equal amounts.

De Ruiter (1956, p.52) emphasised that -

> "the frequency of the captures of prey of a given type depends not only on the releasing value of that type, but also on the number of prey per unit of space and on the hunger of the predator".

He also pointed out that "test prey should not be made the staple diet of the predator because monotony of diet might make them gradually less attractive". In this experiment, population density was held to one crab/box, i.e., two prey per experimental area, while hunger was controlled by only using appetitive predators. Although the test prey were the predators' staple diet after the start of the experiments, with four octopuses there was no suggestion of the animals tiring of them. All four individuals made immediate parachute attacks and eagerly consumed *N. ursus* from the first to the fiftieth trial. However, after trial 47, octopus 25 stopped searching and only resumed after being offered a *Hemigrapsus crenulatus* in the home area. This animal subsequently died after completing 48 trials.

The experimental procedure resulted in the restriction of the two prey types to a *certain area* and *habitat type* of the predators' 'home range' and meant that crabs were exposed only to a *searching* octopus, who in addition was *conditioned to expect* food in that area. With the addition of control trials, this laboratory situation, although contrived, mirrors extant field conditions where selection pressure will be exerted by *searching* predators who, on the basis of prior experience, will be *conditioned to expect* that there may be prey in a *particular habitat* type of a *certain area* of their home range. The pre-training procedure also had the added bonus of negating the effects of novelty. A similar effect against predators conditioned to expect food in an experimental cage, was demonstrated by de Ruiter (1952) using countershaded caterpillars as prey and Jays as predators.

The foregoing discussion has served to emphasise that, in many field situations, the conditions for the incidence of selection of *N. ursus* by possible predators, parallel in important respects those provided by this laboratory experiment.

Two further points which merit discussion and which concern all behavioural experiments, especially laboratory ones, are the effect of the experimenter's manipulation of the experimental apparatus. Wells (1978)

presents a discussion of these problems and concludes that -

> "it is probably adequate that the observer attempts to 'mechanize' himself as far as possible and that he remains out of sight of the octopus until it has attacked the target".

The use of screens and the joining of the two threads (so that the crabs moved equally together) in the foregoing experiment fulfils both these criteria. The addition of view holes in the screens ensured that the potentially valuable information concerning the octopus's behaviour prior to, and during, an attack was not lost. Wells also concluded that confident octopuses, engaged in easy or well-learned discriminations, will continue to discriminate reliably more or less regardless of the ham-handedness of the experimenter and the manner in which the targets are moved about.

An important criticism levelled against the majority of experiments of this type is that not enough overall results were obtained to enable statistical analyses, or that the data so analysed took no account of individual differences between the predators used. The use of the repeated single-case design in this experiment obviates these two criticisms.

15.4.6 How is Visual Eucrypsis Achieved by the Mask?

Visual eucrypsis is commonly (Friedmann, 1944; Robinson, 1969; Emlen, 1973; Edmunds, 1974) thought to be achieved via one or more mechanisms from three basic groups: homochromy, disruption of the body outline, and changing the effects of incident light on the body (i.e., shadows).

Homochromy is a device whereby the animal "resembles the uniform colouration of its background when at rest" (Robinson, 1969). The resemblance may not necessarily be one of hue, but of tone (i.e., intensity), or reflectance (Friedmann, 1944). In reality, the question of whether homochromy is achieved by the tone, hue, or reflectance of light at extreme ends of the spectrum is irrelevant in the case of *N. ursus* and probably many animals which achieve their crypticity by the use of adventitious materials. As these animals are covered by the background materials, it follows that they must also be endowed with the inherent visual properties of the background.

There is good evidence to show that homochromy protects only when the background matches the animal's colouration. But backgrounds change, so species are faced with the problem of correspondingly changing their crypticity. Masking behaviour, although extremely stereotyped in its form, allows tremendous plasticity in the resultant mask; consequently, a potentially diverse range of habitats can be utilised by the crabs. This plasticity is the result of two factors: the mask is constantly renewed, at a turnover rate of approximately 20% / 24 h (McLay, pers. comm.), and a diversity of materials are applied, the only restriction being the crab's ability to tear and apply a particular material. This constancy of renewal results in the crab always bearing some proportion of the background.

This experiment has merely served to show that masked *N. ursus* bearing a mono-species mask (*Halopteris spicigera*), were protected when they were in a matching mono-species environment. However, this situation represents only one of a multiplicity of possibilities. Do these crabs still blend with their background when they have a combination of species in the mask and/or in the background? Are they still protected when the mask consists of a single species, say *H. spicigera*, and the background of another single but totally different species, say *Corallina*? These questions are discussed (with the conclusion that these crabs are still protected) later in this chapter when I consider the behavioural correlates of crypsis. Assuming for the present that the application of a material ensures a blending with a background composed of that or similar materials, then the diversity of materials which *N. ursus* can apply affords a wider scope for the backgrounds which can be safely utilised.

These two attributes are also present in other animals which utilise adventitious materials, but not to the same extent as found in *N. ursus* and probably other masking crabs. Other groups either have a fixed number of times they can change the materials used or the materials they can use are fixed. For example, the bag or case moths *Liothula omnivora* have been observed to use a variety of adventitious materials in their protective cases (Ooi, 1967) but they only build the case once and then their subsequent pupation prevents them from changing it. Conversely, caddis flies (Edmunds, 1974) continue to add materials to their protective cases, but they are restricted to using stone chips.

A variation on the homochromy theme, is the use of 'disappearing' (Friedmann, 1944) or 'flash' (Edmunds, 1974) colouration. These involve revealing bright patches or patterns when in motion, and then suddenly concealing them when coming to rest. This ploy is presumed to confuse a predator who had previously been chasing something bright and conspicuous. The bright red chelae, with their attendant white patches, and the blue and white ventrum of *N. ursus* make this an appealing possibility. Although this aspect has not been investigated experimentally, the mask and body or orientation of *N. ursus* concealed the contrasting body markings when the crab was at rest and exposed them when the animal was moving. The longer pieces applied to the anterior of the crab probably serve to conceal the chelae and mouthparts which, by virtue of the absence of specialised attachment hairs, are not masked (possibly because adventitious materials would hinder the functioning of these parts).

Concealment of body contours. Since it is probably that predators recognise prey by certain characteristic features such as the rounded body, legs or eyes (Robinson, 1969), simple colour resemblance may not be sufficient to prevent a predator from detecting an animal. Outline can be concealed by fusion so that the outline appears smooth and continuous (e.g., Ghanian mantids, Edmunds, 1972). It is possible that the application of the mask so that all the pieces face in one direction (anteriorly) producing a continuous body of algae, even when uplifted by the water, may in fact achieve this 'fusion' effect.

Shadows. If it is advantageous to merge into the background, then clearly it is advantageous to throw no tell-tale shadows. Shadows may be eliminated morphologically or behaviourally.

(i) Substrate shadow. Light will cast a shadow on the substrate and, when from an oblique direction (as occurs at dawn and dusk, especially underwater), the shadow may be very large and hence very conspicuous. This shadow is minimised by dorso-ventral flattening. Reduction of shadow can be further enhanced by laterally directed angled flanges (Edmunds, 1974). The distribution and directionality of the algal mask over the anterior end of *N. ursus* support the hypothesis that the mask also serves to reduce the shadow caused by the anterior region of these crabs, particularly the chelae which are especially prominent in the males. This hypothesis suggests a comparison of the length of the algal pieces attached to the anterior end with the distance of the extended chelae.

This study would be of particular relevance to adult males who have comparatively long chelae (see Plate 1.2).

Obvious shadows can also be eliminated by the behaviours of crouching low, or the preferential distribution of individuals into depressions in the substrate. In Chapter 7 it was shown that *N. ursus* commonly inhabits holes and depressions both on the underside of rocks and on the substrate in general. Crouching behaviour in *N. ursus* is elicited by several stimuli all of which can be related to the reception of stimuli from a predator (see Chapter 8). Shadows can also be minimised by proper alignment of the body. The head down alignment shown by *N. ursus* on vertical walls (Chapter 8) may well serve to eliminate shadows from top lighting.

(ii) Countershading. Shading caused by the illumination of the opposite side of an animal can be counterbalanced by having darker tones where the light strikes and paler tones on the parts in shadow, and this phenomenon is known as obliterative shading or countershading (de Ruiter, 1952, 1956). The mask of *N. ursus* has no evident countershading function. However, in the dim light inhabited by these crabs, shading and consequently countershading, would be less extreme than that in terrestrial daylight. But, in view of the extremely strict balance of tones and an even more stringent control of the placement of those tones required by countershading, the algal mask with its inherent plasticity of form, tone, colour (and even, at times, amount) does not seem conducive to the hypothesis that it serves to countershade *N. ursus*.

(iii) Constructive shading. Shadow, derived from the amount of difference in tone and colour of immediately adjacent parts of the overall pattern, can be used to create illusory pictorial relief on an animal's surface. This phenomenon is known as constructive shading (Friedmann, 1944). In the case of *N. ursus*, there are no features which suggest that the mask is a form of constructive shading.

15.4.7 The Effect on Crypsis of a Predator's Hunting Technique

How eucrypsis achieves its effect depends to a large extent on how the predator hunts for and recognises its prey. In view of this, it is necessary to digress slightly and consider how *O. maorum* visually hunts for

N. ursus under the conditions of this experiment. Four hypotheses have been postulated concerning the mechanisms which might be of general importance in the hunting behaviour of predators (Krebs, 1973). During 'hunting by expectation' a predator is thought to learn to expect a certain number of prey items/area and to stop searching after the area has yielded the expected number. The evidence for this type of hunting is equivocal, resulting in an alternative postulate that birds, at least, spend a fixed amount of time/area. Many predators exhibit 'area-restricted' or 'area-concentrated' searching where they tend to continue to search for a while in the immediate vicinity of a prey capture. 'Niche-hunting' is the strategy whereby a predator is believed to maximise its food intake by spending most of its time in the particular types of areas ('niches') favoured by a prey species. De Ruiter (1952), L. Tinbergen (1960) and others have noted a tendency among birds (and it may exist in other groups) to behave as if they gained a mental picture of one type of prey and subsequently noticed creatures fitting this 'search image' more readily than dissimilar-appearing creatures (Chapter 14). In the case of cryptic prey the predator has not only to locate the area where the prey are, it must also be able to actually detect the prey. Consequently, on theoretical grounds one would expect that cryptic devices evolved to combat hunting by search image, which is object-concentrated rather than by the other three hunting techniques which are area-concentrated.

To determine which of the four hunting techniques was employed, it would have been necessary to expose *O. maorum* to a large number of masked and unmasked *N. ursus* against matching and non-matching backgrounds. Unfortunately, the laboratory experiments were not designed this way. Although strictly I did not test for searching image in these experiments, *O. maorum* could only hunt by searching image as the provision of only one 'niche' precluded 'niche hunting' and the insistence upon *O. maorum* executing an immediate attack and retrieval excluded area-concentrated hunting. Hunting by expectation was also excluded as the octopuses were only allowed to take one prey/trial. Finally, the hypothesis that the mask is crypsis against a predator which hunts by the formation of search images is supported by the general biology and behaviour of both *N. ursus* (refer Section I) and *O. maorum* (Chapter 12). However, the existence of a search image hunting technique does not preclude the fact that, in the field, *O. maorum* may also use a combination of all four techniques during hunting.

15.4.8 The Effect of Size on an Animal's Crypsis

Size of an animal has also been noted to influence the effect of its crypsis. Poulton (1887) held that large size alone may protect a species against certain of its smaller predators while L. Tinbergen (1960) found that among highly cryptic caterpillars the bigger species ran a greater risk of capture than the smaller ones. These experiments did not test for the effects of size, and there is certainly no information in the literature to enable a comparison between different sized masking crabs. This question of the effect of size on crypsis could be a very interesting aspect to investigate.

15.4.9 Behaviours Which Enhance Crypsis

The behaviours hypothesised to enhance crypsis have been discussed previously (Chapters 7, 8 and 14). However, as the success of the immobility and match with the background of *N. ursus* in maintaining crypsis against octopuses was actually tested in these experiments, it is now pertinent to discuss the effect of these behaviours.

(a) Movement

Movement is a powerful attention-eliciting stimulus to many predators (Curio, 1976). For example, Kaufman (1974) demonstrated that the owls *Tyto alba* and *Otus asio* preyed on significantly more active than inactive mice, *Mus musculus*, regardless of their match with the background. In view of this, it is generally held (e.g., de Ruiter, 1956; Robinson, 1969; Edmunds, 1974) that the advantage of even the best crypsis is greatly reduced by gross movement such as locomotion, feeding, or display.

The attempt to determine the relationship between the effect of the mask and the crab's immobility was unsuccessful because the octopuses could not be induced to make parachute attacks on distal cues alone, unless the crabs were moving. However, this factor does reinforce, qualitatively at least, that immobility reduces the chances that both masked and unmasked crabs will be detected from a distance. The theory that immobility may enhance crypticity is also suggested by the observation that *N. ursus* respond to predator-like stimuli by immobility (Chapter 8), by crouching lower and gripping the substrate. If unbalanced by the predator, they flexed and remained motionless (see Chapter 8).

However, in the experiment involving moving crabs, mobility was not deleterious to the chances of survival of the cryptic (masked) crabs compared to the non-cryptic (unmasked) ones. Perhaps the crypticity achieved by the mask was sufficient to overcome the disadvantage of the crab's movement? Alternatively, it may be the result of light intensity. The majority of cryptic animals studied have diurnal predators and must maintain crypsis during daylight. *N. ursus*, on the other hand, is anachoretic during the day time so, when it is exposed to predation, the light intensity at best will be comparatively dim. Alternatively, the reason may lie with the experimental design. Ruggiero *et al.*, (1979) investigated the interdependence of prey-associated stimuli using mice (*Mus musculus*) as prey and kestrels (*Falco sparverius*) as predators. Although their experiments are subject to the criticism of small sample size of both predators and prey, these authors were able to demonstrate a significant interaction, for the kestrels, between the movement and morphology of the prey. As my experimental design involved cryptic and non-cryptic moving prey, I was testing two prey characteristics. In the light of the findings of Ruggiero *et al.*, the effects of movement on the maintenance of crypsis would be better tested by comparing the predator's response to one moving and one stationary, but equally cryptic crab. But as previously mentioned, *O. maorum* did not respond well to non-moving prey. Another point worth considering is that in this experiment, the mask and the algal background were homogeneous. It is possible that movement may prove deleterious to *N. ursus* if the mask and the background differ to any extent, from just slightly to totally heterogeneous. This could be tested by comparing the octopus's reaction to moving crabs against backgrounds which were heterogeneous with the mask.

(b) Matching the background

An animal may be cryptic in one habitat, but very conspicuous in another. My experiment, and those of other workers (e.g., Dice, 1947; Kettlewell, 1956; de Ruiter, 1956; Kaufman, 1971) indicate that selection by predators is likely to eliminate any animal which settles in the wrong place. Consequently, it has been postulated that some mechanism that ensures that a cryptic animal is normally able to select the appropriate background to rest on, will be favoured. The choice of an appropriate background by cryptic animals has been demonstrated for moths, grasshoppers, mantids, and nudibranchs (Edmunds, 1974). Unfortunately, the mechanisms ensuring the correct selection of a background by cryptic animals have been difficult to determine.

Masking crabs provide an interesting case for this problem of background selection by cryptic animals. The fact that masking crabs generally matched their background was the major reason for assuming that the mask functions as visual crypsis against predators (Graeffe, 1882; Aurivillius, 1889; Garstang, 1890; Stebbing, 1893; Verrill, 1908; Milligan, 1915; Cott, 1940; Street, 1952, 1966; Schmitt, 1968; Edmunds, 1974; Wicksten, 1975, 1980). It had also been observed that if the type (Aurivillius, 1889) or colour (Wilson, 1935) of the background material was changed, masking crabs changed their mask. Stebbing (1893) postulated that masking crabs were able to perceive discrepancies between their mask and the environment and adjusted the mask accordingly. Minkiewicz (1907, 1909) tested this hypothesis with a series of crude experiments involving changing the background colour and he concluded that *Maja* distinguished the masking materials, not only according to their colours, but chose them in relation to the background colour. Minkiewicz also alleged that this 'preference' persisted a certain time after changing of the background colour. More recently, Schmitt (1968) propounded this view. However, Burgi (1968) put *Maja squinado* and *M. verrucosa* into aquaria which were covered by a coloured fabric, each aquarium being of a different colour. The crabs were then given pieces of string of equal lengths and seven different colours, which were made by pulling threads from the same fabrics as covered the aquaria. In contradiction to Minkiewicz, Burgi found that *Maja* did not choose string of the same colour as the background, nor did they exhibit a preference for any one colour. Also, repeating the experiments in total darkness did not affect the colour of the strings used.

The continual replenishment of the mask by *N. ursus* (20% of the mask/24 h, C.L. McLay, pers. comm.) explains Minkiewicz's finding that the preference for materials of the original background persist for some time. In fact, by extrapolation of McLay's figures, this 'preference' should last approximately five days (120 h). McLay's findings also explain why Bateson (1889), Wicksten (1979) and I have observed that, both in the field and in the laboratory, many individual crabs (of any particular species) do not always have the same materials in the mask as are in the background immediately adjacent to these crabs. The degree of agreement between the mask and the background will be determined by the distance the crab moves and the degree of variation between neighbouring background areas. Consequently, in the field, the mask can vary from 100% in agreement to 100% in disagreement with the background.

In addition, crabs in the laboratory make no obvious attempt to select resting areas where the agreement is 100%. For example, in Chapter 14, where the crabs had an *Halopteris spicigera* mask and the background comprised gravel patches, mixed algae, but mainly *Corallina* spp. and a large patch of solely *H. spicigera*, both masked and unmasked crabs would rest on/in any of the three background types, not only at the beginning, but throughout the entire trial. Several potential explanations can be considered for this lack of agreement between the mask and the background: crypsis is not the primary function of the mask, an exact agreement is not necessary for the mask to function in crypsis, or the individual distances (Chapter 8) maintained by *N. ursus* were larger than the amount of matching background offered.

The finding that the mask was effective against a matching and not a contrasting environment initially suggests that the explanation that crypsis is not the primary function of the mask is correct. But the explanation that an exact agreement between the mask and the background is not necessary is more appropriate if one considers that this experiment has only concerned a comparison between two extremes, the complete agreement between the mask and the background, and the reverse. None of the many possibilities between these two extremes has been considered. The natural environment of *N. ursus*, and most likely other presumably cryptic animals, is not homogeneous. The intertidal habitat contains a multitude of algae, both living and in the drift. Even large expanses of bare rock contained little pockets of drift or the occasional tuft or cluster of tufts of generally heterogeneous algae. Concentrations of one growing species are rare, and even these are not homogeneous as pieces of drift weed, comprising many species, get caught in these mono-species patches. In reality, the crab can be covered with any naturally occurring part of the intertidal environment and not be incongruous with its surroundings. The effect of a homogeneous mask against a heterogeneous background was, in fact, investigated in Chapter 14. Unfortunately, as the mask was subsequently found to depend on light intensity to achieve its effect, the results of Chapter 14 are not valid for consideration here as the light intensity used was too high to allow the attainment of crypsis.

A clue to determining how predators and, in particular, *O. maorum* may respond to a homogeneous or heterogeneous crypsis against a heterogeneous background is provided by a consideration of the selectivity of predatory responses. Eibl - Eibesfeldt (1952) showed that toads (*Bufo bufo*) had to learn that moving blades of grass were inedible; de Ruiter (1952) found

that the interest of European jays (*Garrulus glandarius* L.) was proportional to the number of stick caterpillars presented compared to the actual twigs they mimicked. This suggests that jays have to learn that the twigs are inedible. Assuming that *O. maorum* is capable of this type of learning, then once they had learnt that the alga was not edible, these octopuses would be unlikely to attack every piece of incongruous alga in a complex heterogeneous algal environment. On the same principle, *O. maorum* is unlikely to attack every piece of alga that moves, as in the intertidal area algal clumps and drift algae are constantly moving with the water currents. Certainly, if *N. ursus* has been disturbed, it exhibits a curious rocking behaviour (Chapter 8) which resembles algae wafting in the water currents. This then may help explain why, in the experiments in this chapter, crypsis was maintained even though the masked crabs were moving over the algal clumps.

Kettlewell (1959) hypothesised that, if this selective response by predators is a general phenomenon, camouflaged animals should choose parts of the environment which offer the most unsuccessful encounters. In the case of animals which have a fixed camouflage, they should choose environments which provide an exact match with their eucrypsis. On the contrary, those animals whose eucrypsis is plastic can utilise a range of environments which are similar to the materials used to achieve eucrypsis. Hence, in the intertidal marine environment which *N. ursus* inhabits, the most unsuccessful encounter would be afforded by algae which are more abundant than hydroids and bryozoans, while the reverse would hold true for deeper water. Collections of *N. ursus* from both the intertidal and deeper waters show that *N. ursus* in fact utilise those parts of the environment which offer the most unsuccessful encounters (see Chapter 5).

This heterogeneity of the crabs' environment combined with the selectivity of the predators' response may explain why *N. ursus* (and other masking crab species) in the laboratory do not choose materials to match the background. As the material applied comes directly from their environment then, in the field, these crabs will blend with their environment regardless of the materials used. In consequence, the application of adventitious materials, particularly as used in masking, is probably the most effective form of 'protective colouration' in existence.

In conclusion, at a light intensity of 0.11 foot lamberts in paired presentations against a matching algal background, and in an experiment in which *O. maorum* was constrained to hunt by visual cues, unmasked *N. ursus* were attacked significantly more often than were masked individuals. Consequently, this work provides the first experimental support for the hypothesis that the algal mask of a masking crab functions as visual eucrypsis against a predator. The selective indices obtained ranged from 0.63 to 0.76 making the evolution of masking behaviour readily understandable. More importantly, the mask failed to have an effect on predation at the higher light intensity of 0.54 foot lamberts. This demonstrates that the eucryptic effect of the mask is dependent on light intensity, and it is argued that this is a phenomenon of general significance in the evolution of eucrypsis in animals.

SECTION II

CHAPTER 16

DISCUSSION

The aim of Section II was to experimentally demonstrate that the algal mask of *Notomithrax ursus* conferred an advantage with respect to survival against predatory octopuses. The selection experiments reported in this Section are evidently the first to demonstrate that presumed crypsis, afforded by the application of adventitious materials, does indeed confer a survival advantage against a predator.

16.1 THE PREDATORS

Octopuses were chosen as the predator for these experiments as they are recorded as being major predators on spider crabs. Furthermore, the general biology and predatory behaviour of octopods has been well documented in the literature. In the case of *Octopus maorum* and *Robsonella australis*, this information was supported by a preliminary study of their predatory behaviour. Presumably, *O. maorum* at least, is a natural predator of *N. ursus* as it has the same habitat and nocturnal activity and has been collected in close proximity to this crab. *O. maorum* readily preyed on *N. ursus* in the laboratory and the fact that *N. ursus* were eaten the first time they were presented suggests that *O. maorum* is a natural predator of *N. ursus*. Since *R. australis* rejected the majority of *N. ursus* after they had been captured, either *R. australis* is not a natural predator or the two individuals used were not familiar with *N. ursus* as prey.

Although teleosts, particularly the pseudolabrids, also fulfilled the above criteria, octopus had the most highly developed visual, tactile and chemosensory systems of all. This allowed a greater capacity for determining the mode of expression of the anti-predator function of the mask. Since contrast with the background, rather than colour differences *per se*, was being tested, the lack of colour vision in octopuses was of no

importance to these experiments. Furthermore, octopods have well-developed brains, capable of rapid learning and memory. Their visual system has the added advantage of performing well at low light intensities. There is every probability that if the mask is effective against predators such as these, it will also be effective against other predators with fewer or lesser discriminatory powers.

A combination of the susceptibility of *O. maorum* and *R. australis* to physical and sensory stress, their learning and memory abilities, and their ability to escape easily meant that special equipment and experimental procedures were required to maintain healthy animals and to ensure that realistic data were obtained. Given these proper conditions, the New Zealand *O. maorum* and *R. australis*, like *O. vulgaris* (Wood, 1963) adapt readily to captivity and exhibit behaviour patterns that may be assumed to approximate those of feral individuals. Consequently, the experimental apparatus was especially designed to meet not only the requirements imposed by the general biology of *N. ursus*, but also to meet those of *O. maorum* and *R. australis*.

16.2 METHODOLOGY

Initially, the investigation concerned the observation and analysis of the entire predatory sequences between *N. ursus* and the octopuses. The model derived from the observation of entire predatory sequences is in the form of a conventional flow diagram. Although it includes the main 'decision' or discrimination stages observed, the model remains a gross over-simplification. The model provided a concise method of describing the various courses of the predatory interaction and one which facilitated comparison of the effects of the various factors considered. The sequences discussed were derived from pooled data and, as such, only allowed trends and not individual behaviours to be followed. Furthermore, it must be remembered that the pooling of data tends to underestimate the uncertainty.

The differences between behaviour sequences given to different types of crabs, the effect of differing backgrounds and the influence of prey movement, were investigated using stochastic analysis as recommended by Altmann (1965) and Slater (1973). Presenting the frequencies with which the various courses of the interaction were seen (= stochastic models)

meant that the predictions of behaviour and hence derivation of possible functions were more certain than if based on the assumption that all behaviour patterns had an equiprobable distribution. Although an analysis of the behaviour sequences of the interactions between *N. ursus* and predatory octopuses was a useful initial step to determine the stages affected by crypsis, the method had several disadvantages. For example, the use of free-ranging animals made any statement of the events occurring prior to detection very difficult as masked and unmasked crabs were not equally available to the potential sensory abilities of the octopuses at any one instant. In addition, eucrypsis implies a match with the background, but even the 'natural' background afforded a continuum of matching backgrounds. Although octopuses are predominantly visually oriented hunters, they also possess a well-developed chemotactile sense and at least a potential for auditory discrimination, and the laboratory situation did not allow a determination of which of these senses the mask was effective against.

Consequently, an experiment was designed to test the ability of an octopus to visually detect masked and unmasked *N. ursus* which were moving against a matching background. The method employed was that of a 'discrimination' experiment, modified to ensure that the predatory strategies employed by *O. maorum* were not hindered or exaggerated and so that disturbance from the experimenter was minimised. A common criticism of experiments testing the efficacy of 'protective colouration' is that the behaviour of captive animals toward food has been demonstrated to be an unreliable indication of what wild individuals of the same species would do in the presence of the same food. But these experiments were not testing 'food preference'. Rather, they were testing the ability of a predator to actually *detect* the prey, not choose between them. By matching the colour of the mask and the background, the prey crabs could be made highly cryptic, and since the prey were standardised except for the presence of the mask, factors such as palatability, handling time and search pattern could be ignored. The emphasis in all of these investigations was on the external stimuli provided by the prey. The possible effects of the internal state of the octopuses on their behaviour were controlled for by using only appetitive individuals.

16.3 THE EFFECT OF THE ALGAL MASK

Against a heterogeneous 'natural' background, the algal mask of

free-ranging, previously detected, *N. ursus* hampered direct attacks, triggered by distal cues, by the octopuses. Three times as many masked crabs were attacked against a contrasting background compared to the 'natural' one. Consequently, the mask appears to function as crypsis. Furthermore, as masked crabs were not perceived as inedible against the contrasting background then, under the experimental conditions at least, the mask most likely rendered the crab eucryptic. This hypothesis is further supported by the fact that against the 'natural' background the octopuses were never observed to attack algae after finding and eating a masked crab.

Against a homogeneous matching algal background, the algal mask was effective in preventing the actual detection of *N. ursus* by octopuses constrained to hunt by visual cues alone. This finding corroborates the hypothesis that the algal mask of *N. ursus* renders the crab eucryptic to visually hunting predators. More importantly, the mask was dependent for its effect on the ambient light intensity, being effective at 0.11 foot lamberts but not at the higher intensity of 0.54 foot lamberts. *N. ursus* are nocturnal and photonegative, not emerging from hiding until it is completely dark. The dependence on light intensity suggests that the visual discrimination of octopuses decreases with decreasing light. Consequently, the hypothesis that visually oriented hunters have been important selection pressures favouring the evolution of these activity patterns is supported. Furthermore, Dice (1947) also found that selection was most discriminating at light intensities where predatory owls were just barely able to see their prey. Consequently, the effect of light intensity would seem to be a phenomenon of general importance when considering the evolution of eucrypsis in animals.

The selection indices obtained with predatory octopuses ranged from 0.63 - 0.76, and may be much higher in the field where the prey are not so disadvantaged as in the laboratory. In other experiments, in which the predators were evidently using sight, cryptic individuals enjoyed more than a 20% advantage over conspicuous individuals in escaping capture. Consequently, the evolution of protective colouration, including that by adventitious use, is readily understandable. Assuming that the selection index is at least a rough estimate of the corresponding selection co-efficient, then selection will be intense for the masking behaviour of *N. ursus*. Consequently, the time and energy invested in forming and maintaining the algal mask by a mainly anachoretic animal is also readily understandable.

16.4 HOW THE MASK ACHIEVES ITS EFFECT

Surprisingly, more masked than unmasked crabs were detected and immediately attacked against a contrasting background. This enigma is readily understandable if the results of the discrimination experiment are considered. Against a homogeneous matching background, the octopus was more effective at capturing the conspicuous prey than the cryptic one. Hence, the mask would appear to make *N. ursus* more conspicuous against a contrasting background. As unmasked crabs were matched in size with masked crabs including the mask, this increase in conspicuousness is perhaps the result of some other dimension of the mask.

By virtue of the fact that the material used comes directly from the background, the mask is most likely to achieve homochromy with the background. Furthermore, the continual replenishment of the mask enabled the crabs to achieve homochromy with a wide range of backgrounds. The mask may conceal the body contours by providing a fusion effect. This suggestion is rendered even more plausible if it is remembered that octopuses are reported to make discriminations based on absolute extents. Octopuses classify shapes according to the relation of outline to area and the mask may increase the overall apparent size of the crab, dissuading the octopus from attacking. There is also a possibility that the mask enables the ventral and cheliped markings to be used as flash colouration during flight. Finally, the mask may decrease the substrate shadow thrown by *N. ursus* in the same manner as lateral flanges do - particularly over the chelipeds.

In general, cryptic devices appear evolved to combat hunting by 'searching image' rather than any other method. Octopuses would appear to be capable of this type of hunting as they learn readily and seem capable of both short- and long-term memory. Certainly, the design of the discrimination experiment meant that the predatory octopuses were most likely to be constrained to using a 'search image' when visually searching for the crabs.

16.5 THE DEPENDENCE OF THE MASK ON OTHER BEHAVIOURS

16.5.1 Immobility

The octopuses could not be induced to make parachute attacks on distal cues alone unless the crabs were moving. This suggests that

immobility will reduce the chances of a crab being detected from a distance. Certainly, the major defences of freezing, crouching, hiding, and remaining buried shown by *N. ursus* all involved eventual immobility. In the discrimination experiment the up and down movement of the masked crabs did not appear to nullify the advantage conferred by the mask. This is surprising considering that octopuses respond best to vertical movement, especially at a speed of 2 - 4 movements/sec as in the experiment. This lack of effect of movement may be attributable to the phenomenon of selectivity of a predator's response. Octopuses would be unlikely to attack every incongruous piece of algae in a complex heterogeneous algal environment. This suggests that cryptic prey, especially if crypsis is derived adventitiously, would be best to choose parts of the environment which offer the most unsuccessful encounters. In the case of masking, the crabs will generally do this purely by virtue of the fact that they appear to use whatever is at hand rather than preferring certain materials.

An interesting point to note is that some birds and primates are capable of finding immobile, cryptic prey (Robinson, 1969). For example, Dice (1945, 1947) showed that two species of owls could detect the presence of dead, cryptically coloured mice at very low light intensities. The nature of the cues used in prey recognition when the prey is immobile has not been elucidated. However, birds and primates possess colour vision, while octopuses do not. Perhaps colour plays a part in detecting motionless prey.

Although the presence of the algal mask did not affect the behaviour of *N. ursus*, their defensive behaviour was significantly different from that of non-masking crabs. *N. ursus* had a greater tendency to remain immobile. Seven times as many *Hemigrapsus edwardsii* and *Petrolisthes elongatus* moved when contacted compared to *N. ursus*.

16.5.2 Spacing

Doubling the density of available prey presented against the 'natural' background by adding the two non-masking species *H. edwardsii* and *P. elongatus*, nullified the effect of the mask. This effect of density corroborates the hypothesis advanced by Tinbergen *et al.* (1967) that cryptic prey should disperse to lower their chances of detection. Captive octopuses could detect some masked *N. ursus* as far as 78 cm away

(at 0.11 foot lamberts light intensity). However, these crabs were often within 20 cm of each other during their active phase in the field. This relative lack of inter-individual spacing can probably be attributed to the polymorphism achieved by continually changing the mask. Being polymorphic lessens the chances of the predator learning the characteristics of the prey and so hinders the formation of a 'search image'.

16.5.3 Choice of an Appropriate Background

These experiments, particularly the discrimination experiment, have indicated that selection by predators is likely to eliminate any animal which settles in the wrong place. *N. ursus* made no attempt to select resting areas which provided a good match with the mask. However, any animal covered with a naturally occurring part of its normal environment, such as masked *N. ursus* amongst the intertidal algae, will not be incongruous with its surroundings. Consequently, with respect to the choice of an appropriate background at least, it can be argued that crypsis will be better achieved by adventitious use than by some intrinsic character(s) of the possessor.

16.5.4 An Appropriate Resting Attitude

The complex heterogeneity of the intertidal environment would seem to account for the lack of effort by *N. ursus* to align itself in any particular way when on a horizontal surface. However, the posterior uppermost position when on a vertical surface seems to make use of the long algal pieces applied to the anterior. These pieces cover the unmasked, chelipeds and oral region, reducing the effects of shadows. The effect of shadows was also lessened by their behaviour of crouching when at rest or when threatened by predator-like stimuli.

16.6 THE EFFECT OF CONTACT BY THE PREDATOR

Octopuses possess complex chemotactile systems. They can distinguish objects by touch as rapidly as by sight in some instances. Hence, it was possible that the mask rendered the crabs cryptic to the tactile sense of octopuses. Physical differences are distinguished by the distortion imposed on the suckers. Although octopuses cannot distinguish shapes, weights or size by touch, they can discriminate

between objects which differ only in the arrangement of such irregularities. Given this information, it was plausible that the masked crabs present a different sucker distortion than unmasked ones. As the mask is changed, so would the irregularities perceived by the octopuses, hampering the formation of a searching image. Octopuses also have chemotactic capabilities. Since octopuses can detect minute concentrations of substances dissolved in sea water, the mask is unlikely to render *N. ursus* cryptic to the chemotactile sense of this predator. After contacting *N. ursus*, the octopuses failed to differentiate between masked and unmasked individuals. Consequently, the mask is unlikely to be a primary defence of a proximal tactile or chemical type against these predators.

The mask affected neither the capture nor consumption of these crabs by any of the 26 octopuses tested. Also, none of the octopuses avoided further contact with masked crabs after previously capturing one. Consequently, the mask is unlikely to be a secondary defence by virtue of any inherent noxious or toxic properties. Masked crabs were eaten as readily as unmasked individuals, so the difference in response to these crabs against a natural background was not attributable to any difference in palatability between them. Consequently, the mask was very unlikely to function as aposematism.

Although the mask was not effective in deterring a capture once a crab was contacted, the animal's subsequent behaviour increased its probability of survival. If possible, *N. ursus* would withdraw to a retreat, such as a crevice in the rock or among the branches of an algal clump, from which octopuses had difficulty in extricating them. Otherwise, when contacted these crabs would flatten hard against the substrate and freeze while applying a powerful grip to the substrate. If rolled onto their dorsal surface during the attack, *N. ursus* immediately flexed all their appendages in towards the ventral midline and froze, forming a motionless ball (flexion). Immobility, as occasioned by freezing and flexion, was the most commonly exhibited defence and is especially important against a predator such as octopus which relies so heavily on movement as a cue for prey discrimination.

16.7 COMPARISON WITH NON-MASKING CRABS

Both masked and unmasked *N. ursus* elicited the same predatory

responses from the octopuses as the two non-masking crab species provided. Hence, both masked and unmasked *N. ursus* are responded to as crab-type prey. However, by virtue of their greater tendency to become, or remain, immobile, *N. ursus* were less likely to be attacked than the non-masking species.

N. ursus were no more palatable to the octopuses than the non-masking crab species. This finding is contrary to Kettlewell's (1959) hypothesis that there was a direct correlation between an animal's degree of crypsis and its degree of palatibility to a predator. However, since neither *H. edwardsi* nor *P. elongatus* were noticeably aposematic, this may not be a fair comparison for testing Kettlewell's hypothesis.

16.8 THE EFFECT OF INTRINSIC BODY CHARACTERISTICS

Unmasked crabs were attacked against a contrasting background. Consequently, at a light intensity of 0.54 foot lamberts the intrinsic body characteristics are unlikely to be a special protective resemblance. Since eucrypsis of the mask was effective at the lower light intensity (0.11 foot lamberts), a special protective resemblance of the body characteristics may also be dependent on light intensity. However, this is unlikely as unmasked crabs look very crab-like to humans at this intensity against a contrasting background. Unmasked crabs were not protected against the homogeneous algal background at either light intensity, suggesting that the body characteristics were not eucryptic either. However, the homogeneous background did not 'match' the unmasked crabs *per se*. The body characteristics may render the crab cryptic against patches of sand or silt devoid of algae.

16.9 EVALUATION OF THESE EXPERIMENTS IN RELATION TO THE FIELD

To guarantee encounters between *N. ursus* and predatory octopuses and to enhance the chances of observing the entire interaction, the animals were observed in the laboratory rather than in nature. However, some degree of artificiality is always present in laboratory experiments. The most abnormal effect of the testing conditions for both the predator and prey was the restricted space of the tanks. In nature, the octopus's hunting area is presumably much greater than in the laboratory, and when an individual loses interest in a stimulus it probably moves to another

area rather than staying in the vicinity as it is forced to do in the laboratory. In addition, crabs in nature have a chance to move away from the 'danger' area. Furthermore, during the observations of free-ranging animals, the limited space on the experimental tray often resulted in the crabs being in closer proximity than was natural during their active period. However, in the discrimination experiment the crabs were 19.5 cm apart which is approximately the minimum distance that *N. ursus* maintain in the field during the active period.

- - -

While the results support the existence of a potential selection pressure of the kind required by the hypothesis, they do not give information about the effectiveness of this pressure under natural conditions. However, the species used are probably representative of a vast array of species with similar habits, while the conditions of these experiments probably diminish rather than enhance the selectivity of feeding. Certainly, the chances of an octopus capturing an inconspicuous *N. ursus* are probably greater in an experimental tank than in the intertidal area.

CHAPTER 17

GENERAL DISCUSSION

17.1 CRYPSIS AS A RESULT OF MASKING

Like many Majidae, *N. ursus* actively selects, cuts and attaches adventitious materials to its dorsal surface. As masking crabs generally blend with their background, the mask has been assumed to make the crab eucryptic. However, substantiating data have been lacking. The central aim of this thesis was to consider in some detail evidence pertaining to the hypothesis that the algal mask of *N. ursus* renders the crab cryptic and thus protects it from visually oriented predators. Masking crabs are especially interesting for study as the mask is not an intrinsic bodily feature but is acquired extrinsically.

The first step in determining the function of a character in a Darwinian sense, is to determine that the character is most probably an adaptation of the animal rather than an exaptation (Gould & Vrba, 1982) or pleiotrophic effect. Consequently, Section I of the thesis was concerned with determining if the algal mask fulfilled the criteria expected if it functions to make the crab cryptic. Also, an effort was made to uncover the potential selection pressures responsible for shaping the evolution of masking. Observations and experiments, both in the field and the laboratory, revealed that *N. ursus* invest a considerable amount of time and energy during all stages of its life history, in forming and maintaining the mask. These data lead to the conclusion that masking is indeed an important adaptation. Furthermore, the data suggested that the mask was most likely to render crabs eucryptic with respect to their background and that predators, in particular octopuses, were most likely to be responsible for the evolution of masking.

The second step in determining the function of a character is to explain why the character in question is maintained as a normal characteristic of the species and not allowed to degenerate. Consequently, the aim in Section II was to provide experimental evidence that the mask performed the function that the hypothesis demanded of it. Systematic observations of interactions between *N. ursus* and octopuses demonstrated

that the algal mask impaired the orientation and/or triggering of attack by the predators based on their reception of distal cues. In addition, the use of differing backgrounds confirmed that the mask most likely functions as eucrypsis rather than special protective resemblance. Furthermore, these observations demonstrated that the effect of the mask was apparently interrelated with other behaviours of *N. ursus*. Being widely dispersed and remaining immobile probably greatly enhanced the effectiveness of crypsis.

The discrimination experiment showed that the mask was very effective at preventing *N. ursus* from being detected against a matching background when the octopuses were constrained to hunt by visual cues. An important finding which warrants particular emphasis is that the mask was dependent for its effect on ambient light intensity. Although highly effective at a light intensity of 0.54 foot lamberts, the effect of the mask was nullified in brighter light (0.11 foot lamberts). The importance of light intensity on the effectiveness of eucrypsis is probably a phenomenon of general significance in the evolution of eucrypsis in animals. In addition, the discrimination experiment corroborated the hypotheses that a match between the mask and the background, and immobility by the crab, enhanced the effect of crypsis.

One of the firmest possible demonstrations that natural selection maintains the form or value of a trait is provided by evidence that natural variation between individuals is associated with differential reproductive success. Long-term studies on the effect of protective colouration on reproductive success have been conducted by Curio (1973) and Bantock *et al.* (1976). In most studies, calculation of reproductive success would be extremely difficult and currently impractical. This was true for the present study of *N. ursus*. However, from laboratory studies it was possible to determine the effect of the mask on survival. This permitted calculation of selection indices. These indices should give at least a rough estimate of the effect of the mask on survival in nature and of the selection co-efficients, which of course are related to reproductive success rather than simply survival. The selection indices obtained were high (0.63 - 0.76), suggesting that selection co-efficients in the field are quite large.

The algal mask of *N. ursus* is a particularly effective form of crypsis, by virtue of the fact that it is adventitious. Utilising

materials from the background has the advantage that the match will be close to 100%, as the mask has all the characteristics of that background, rather than having to simulate them. This effect applies regardless of the sense(s) used by the predator to locate its prey.

N. ursus enjoy the added advantage of being able to change the mask continually. Consequently, they can utilise a wide range of backgrounds. This advantage is further enhanced by the fact that most predators habituate and cease responding to neutral stimuli. Secondly, a predator's discriminative ability is limited by unpredictability. It cannot tune its selective response to the mask beyond a certain level of precision because the mask not only varies between individual *N. ursus*, it also changes from day to day with respect to one individual. This, of course, would hamper the formation of search images by predators.

17.2 FURTHER RESEARCH

The experiments reported here have only concerned totally masked or unmasked *N. ursus*. There has been no investigation of the advantage of varying degrees of algal cover. For example, in Section I the results from the study of the occurrence of masking indicated that there was a correlation between the probability of being covered and the amount of sharply defined outline of a body area. This suggested that the mask may disguise the body outline. This hypothesis could be investigated further by exposing crabs with various parts of their dorsal surface covered, and with totally masked and unmasked individuals, to predatory octopus. Similarly the importance of the degree of matching with the background could be investigated. In these experiments both masked and unmasked crabs were presented against backgrounds which either provided a good match or contrasted greatly. This type of study would be especially important for a determination of whether or not the body attributes of unmasked *N. ursus* allow a special protective resemblance against homogeneous sandy backgrounds.

There are many further points to be elucidated concerning the effect of the ambient light intensity too, as well as the effects of the background, spacing, and movement of the crabs on the effect of light intensity. For example, repeating the interactions between free-ranging

N. ursus and predatory octopuses at the lower light intensity should provide more information on the question of whether the mask makes the crab eucryptic or gives it a special protective resemblance.

Ross & Boletzky (1979) found that the pagurid *Dardanus arrosor* loses its transfer activity towards its symbiotic actinian *Calliactis parasitica* after a long confinement in an aquarium not containing octopus. However, the activity of transferring the actinian to its dorsal exoskeleton returned when the pagurid received only the effluent from a tank containing one of three species of octopus, or a cuttlefish species. The activity toward the actinian did not return when visual cues only were provided. It was noted that when *N. ursus* were kept in the laboratory for long periods, they also gradually stopped masking even though fresh algae were continually supplied. Since this behaviour may have been the result of the lack of cephalopod effluent, an experiment of the type conducted by Ross & Boletzky might be worthwhile. Alternatively, the decrease in masking behaviour might have been a result of stress induced by long-term captivity.

17.3 DEFENCE AGAINST OTHER PREDATORS

An adequate picture of the importance of the mask in the natural environment would require a knowledge of the share of each predator in the total mortality of *N. ursus*. Furthermore, a knowledge of the effect of the mask on each of the visual and possibly chemotactile predators acting on the population would be necessary. In addition, the effect of the mask should be studied on a representative sample of *N. ursus* rather than being restricted to a single intertidal population. However, a study of this magnitude would be extremely difficult and currently impractical for most studies of the efficacy of concealing colouration. This was also true for the present study of *N. ursus*.

However, some idea of how crypsis works against predators in general can be gained by using different types of predators. For example, Sumner (1934, 1935a, b) used two bird species and one fish as predators to demonstrate the cryptic effect of changes in skin colour of the fish, *Gambusia patruelis*. Only one type of predator, octopuses, was used in the present study. Initially, two species were used, but only *O. maorum* was used for the discrimination experiment. Hence, any

generalisation of the results to other predators would be open to doubt. Consequently, it would be worthwhile to repeat the above study using other types of predators.

Fish may be important predators of *N. ursus*. It has been argued that reef-living teleosts have been major selective agents in the evolution of cryptic patterns of many octopuses (Nixon & Messenger, 1971). In addition, these fish possess colour vision (Breder, 1946; Nixon & Messenger, 1971) and they are visually oriented hunters which attack moving objects (Stein & Magnuson, 1976). Elasmobranchs orient toward prey by using a combination of auditory, chemical and visual cues (Moeller *et al.*, 1972). Furthermore, elasmobranchs are more active at night; and they possess a high sensitivity to contrasts of light and shadow, as well as motion, when there is a minimal amount of light entering the eye.

Although the eyes of fish are similar to those of octopuses (Russell-Hunter, 1968), their visual acuity, although good, is not as good as that of octopuses. Consequently, the mask may deceive fish more easily than octopuses, especially as octopuses have unusually sharp vision in all respects.

Preliminary experiments with pseudolabrid fish in Section I revealed that the algal mask of *N. ursus* may function as defence 'autotomy'. Some especially interesting experiments could be conducted with fish to determine if the mask does indeed have this function, and exactly how the mask achieves this effect.

17.4 REBUTTAL OF COMMON OBJECTIONS TO THE THEORY OF CONCEALING COLOURATION

There has been some difference of opinion among biologists concerning the effectiveness of concealing colouration in animals. Cott (1940) outlined the major objections which have been raised. Since the information, derived in this thesis, concerning the effect of the algal mask of *N. ursus*, allows a rebuttal of these objections, they will be discussed in turn below.

Objection 1: Cryptic resemblances are incidental effects rather than adaptive modifications.

The study of the incidence of masking among intertidal *N. ursus* revealed that these crabs invest a great deal of time and energy in forming and maintaining the algal mask. Masking behaviour was exhibited by the smallest crabs found and was continued throughout the entire life by both sexes. Furthermore, the acquisition of a mask had priority over other maintenance behaviours. Both moulted crabs and those otherwise deprived of their mask replaced it as soon as they were physically able. In addition, there was no evident variability in the number of algal pieces used in the mask and their pattern of application among *N. ursus* (C.L. McLay, pers. comm.). These facts would not be expected if masking behaviour were a pleiotrophic or other incidental effect. Rather, masking seems to be directly subject to strong selection pressures (i.e., it is an adaptation).

Objection 2: Cryptic colouration is the direct result of physical or chemical causes.

The objection has been raised that colours may be the direct effect of, for example, what an animal has eaten as opposed to the need for concealment. For example, certain caterpillars are green by virtue of the green pigment in their food (Poulton, 1890). In the case of adventitious materials, the anology to this is that the materials have settled passively. This objection can be dismissed for *N. ursus* as the mask is actively cut and applied rather than settling on the crab fortuitously.

Objection 3: Animals which lack concealing colouration appear to fare as well in nature as those which possess it.

The results presented here, particularly those from the discrimination experiment, show that the algal mask conferred a considerable advantage on its possessors. The selection indices obtained ranged from 0.63 to 0.76 and, as the masked crabs were more disadvantaged than they would appear to be in the field, the selection index for masking in nature is likely to be even higher. Certainly other workers have found that cryptic colouration

confers at least a 20% advantage on individuals possessing the cryptic colouration being investigated. The experiments by Kettlewell (1958) were actually carried out in the field and his data provided a selection index of 0.73.

Objection 4: Animals do not restrict themselves to backgrounds which they resemble.

It is true that *N. ursus* do not restrict themselves to backgrounds which provide a good match with the environment. However, since the material they use to form the mask comes directly from their immediate environment and, in nature, this environment is very heterogeneous, *N. ursus* are unlikely to be conspicuous.

Objection 5: Supposed cryptic resemblances are developed beyond the point of usefulness.

Masking is certainly a highly developed behaviour. The actual amount of adventitious material needed in order for the mask to deceive the predator was not investigated (see earlier). However, as a lessening of selection pressure leads to greater variability of a character, the lack of variability of masking would suggest that this behaviour has not developed beyond the point of usefulness. Furthermore, the experiments suggested that octopuses provide a natural selection pressure. Also, these predators possess good visual acuity. Crypsis of the complexity attained by masking would be expected.

Objection 6: 'Protected' animals are subject to attack by keen-sighted predators which are not deceived even by the most perfect cryptic resemblances.

Firstly, the theory of 'protective colouration' does not imply that any group showing protective (or warning) colours is immune from attack by predators. Rather, the theory relies on the supposition that a predator will take the less adapted of two individuals. In the case of crypsis, the more conspicuous animal will be taken. Gradually, as the more conspicuous animals are weeded out, the population as a whole becomes

more cryptic. In essence, the theory does not imply that protection is all-or-none. Rather it is a matter of relative degree.

Certainly, this experiment confirmed that octopus predators take the more conspicuous of two *N. ursus*. In addition, the theory of protective colouration would predict that even if all the crabs were masked, individual variability would mean that some were attacked as they were more conspicuous.

Objection 7: Concealment depends upon immobility rather than upon colouration.

Movement was not a hindrance to the function of the mask in the discrimination experiment. At a low light intensity, masked *N. ursus* enjoyed a 63 - 76% advantage even though they were moving. But the unmasked crabs were also moving. A real test of the effect of immobility would be to expose paired moving and immobile masked *N. ursus*, and paired moving and immobile unmasked *N. ursus* to the octopus predator. In this case the advantage may be reduced, but it is unlikely that it would be nullified.

Objection 8: Concealing colouration cannot be adaptive since many animals lack colour vision.

There is convincing evidence that octopuses lack colour vision. However, masked *N. ursus* were protected against these predators under dim light and against a matching background. Furthermore, crypsis need not depend upon the matching of colour (i.e., hue). It may instead achieve a matching of intensity, reflectance, or polarisation of light.

Objection 9: Cryptic colouration cannot be effective against predators which hunt by non-visual means, nor against visually oriented predators hunting in dim light at night.

Concealment by colouration is irrelevant against predators which do not use the visual sense while hunting, and the criticism itself seems trite. However, visual cues are indeed used by many predators who hunt mainly by senses other than vision, so colouration may still aid the prey.

Although colour differences *per se* may be lost at low light intensities, differences in tone are not. Consequently, protective colouration may still be effective against visually oriented predators which are nocturnally active. Certainly the mask was effective in very dim light against the nocturnal, visually oriented octopus predators.

Objection 10: The theories of adaptive colouration are based upon anthropomorphic concepts.

It is indeed a just criticism that the theories of protective colouration arose from the pervasive assumption that what deceives humans will likewise deceive other classes of predators. However, this assumption may not be particularly unrealistic. The visual systems of many vertebrates are very similar to that of humans. Certainly experiments by Carrick (1936), Isley (1938), Sumner (1934, 1935a, b), Dice (1945), and Kaufman (1973) have demonstrated that attributes, assumed to be cryptic on the basis that they deceive humans, are protective colourations against birds and teleosts. In addition, octopuses have a visual system remarkably like that of humans. The algal mask of *N. ursus*, which renders these crabs cryptic to humans, was certainly effective against octopus predators.

17.5 THE PHYLOGENY OF MASKING

In Chapter 1 it was mentioned that any biological fact can be considered in terms of four different but interrelated types of questions. The questions concerning mechanisms of masking have been studied for *N. ursus* by C.L. McLay (pers. comm.) and Pack (1975). Lebour (1927) dealt briefly with the ontogeny of masking behaviour in several majid species. This thesis has dealt with the adaptive function of masking in *N. ursus* and considered the generalisation of the findings in terms of other masking majids. However, the phylogeny of masking still remains to be discussed.

While observations and experimentation on a single species can suggest functions for behaviour patterns, hypotheses about the phylogenetic origins of these patterns are best formulated following comparative studies. The comparative approach involves the comparison of species in

which the character is present with those in which it is not, and trying to find correlated circumstances that could account for the distribution of the character (Cullen, 1957). Evidence of this type was detailed by Wicksten (1980) who compared various species of spider crabs which masked with species which did not. She found that non- or partial maskers were large, or had cryptic (to the human observer!) exoskeletons or inhabited the stipes of giant algae or soft substrates. From this comparison she hypothesised that the mask functions to camouflage the crab, probably providing protection against predators in all species, and definitely facilitating prey capture in species which were active predators on prey possessing good visual acuity.

Masking presents an interesting evolutionary problem. What are the possible intermediate types between the completely masked forms and the presumed unspecialised ancestral stock? In addition, how did the acquisition of material first occur and how could it have evolved as a forerunner to the behaviour of actively applying materials (i.e., masking behaviour)?

The comparison of masking behaviour among majids also led Wicksten (1980) to formulate a hypothesis to explain the steps involved in the evolution of masking behaviour. In brief, the activities involved in the application of the adventitious materials in the mask are identical with some of the activities involved in feeding. This led Wicksten to hypothesise that masking probably began with early spider crabs that picked edible particles out of the detritus. Eventually, some of these early spider crabs may have begun storing food on their hooked setae, in the manner of the living majid, *Podochela hemphilli*. Wicksten then surmised that the habit of attaching food to the exoskeleton may have given a selective advantage to the early crabs by hiding them from predators, and some of them may have made the transition to attaching non-edible materials for camouflage alone. As an example, Wicksten cited *Loxorhynchus crispatus*, a living majid which seldom eats anything that it has attached to its exoskeleton. In fact this crab often decorates with materials that few marine animals eat, including noxious sponges and stinging hydroids.

Some living spider crabs mask only sparingly, or not at all. Wicksten maintained that some of these species (e.g., *Pugettia producta*) may have largely lost the decorating habit in response to environmental

pressures. Other species (e.g., *Chionoecetes tanneri*) whose soft-bottom habitat lacks decorating materials, may never have evolved the decorating habit. In addition, some spider crabs that do little active masking get covered passively through the natural accumulation of detritus in their hooked setae or through the settlement of encrusting organisms. Wicksten cites as an example, *Scyra acutifrons* which masks only its rostrum. The remainder of the dorsal exoskeleton is covered by sponges or ascidians that settle of their own accord.

Selection for a concealing feature in a prey organism depends upon at least one important predator being more effective at capturing the conspicuous phenotype(s) than at capturing the cryptically coloured phenotype. The experiments reported here demonstrated that octopuses were more effective at capturing unmasked than masked *N. ursus*. Given the passive acquisition of debris and the similarities between the behaviour sequences involved in feeding and masking, the steps to the classic masking behaviour are not too difficult to envisage. When the addition of adventitious materials first occurred, either fortuitously or planted as a foodstore, those without a 'mask' gradually became more and more conspicuous compared to the background. Since the more conspicuous crabs would be more readily captured, the population would become more and more heavily masked until its advantages were outweighed by its attendant disadvantages.

Some majids (e.g., *Stenocionops furcata*) actively attach anemones (e.g., *Calliactis tricolor*) to their dorsal exoskeleton. The transfer behaviour by *S. furcata* has been described by Cutress *et al.* (1970) and this behaviour also shares many attributes with feeding behaviour. Consequently, it is likely that the application of anemones evolved in the same manner as the use of algae. However, although anti-predatory, the defence is most probably the effect of noxious properties of the anemones rather than crypsis.

ACKNOWLEDGEMENTS

I am indebted to my supervisors for their help and encouragement. Dr Colin McLay for introducing me to *Notomithrax ursus*, help with the ecological study, computing and for reading the manuscript. Dr Robert Jackson for help with the behaviour work, valuable discussions of evolutionary theory and for reading the manuscript. Dr Laurence Field for help with the design of equipment and methods used in this study and for ensuring a high level of precision in all of the work. I also thank Professor W.C. Clark and my colleagues from the Australian Society for the Study of Animal Behaviour for their continued support.

The co-operation of all the departmental technicians is greatly appreciated. I also thank Jack van Berkel for technical help at Edward Percival Field Station and Fay Thompson for help with computing. Special thanks are due to Gavin Robinson for his willingness to help with all aspects of this study.

A number of fishermen, particularly Brent Fearnley and Douglas Posa, provided me with access to both predators and prey. Without their co-operation and assistance the study would not have been possible.

Special thanks are due to Pauline Taylor for the magnificent job made of typing the final manuscript. I am also grateful to Penelope Richards for the final reproduction of the illustrations and Joan Buckley, Terry Williams, Richard Rowe and the staff at 'ColourTrue' for the photographs.

Thanks are also offered to all those friends and colleagues who have contributed to this thesis, in particular, Jan McKenzie, Jeanette Bowie, Marcus Simons and Simon Bloomberg.

The study was supported in part by a New Zealand University Grants Committee Scholarship.

I am indebted to my parents, Ivy and Albert Pack, for their financial assistance and their continued faith in me. Many thanks are also due to my husband, David Shorter, for his financial support and help with field collections, making equipment and performing some experiments. Finally, a very special thank you to my mother, Ivy, who was never daunted by any request for help, lending a friendly ear, typing numerous drafts and proof-reading the entire manuscript.

REFERENCES

AL-ADHUB, A.H.Y. & NAYLOR, E. (1975). Emergence rhythms and tidal migrations in the brown shrimp *Crangon crangon* (L.). *Journal of the Marine Biological Association of the United Kingdom 55*: 801-810.

ALCOCK, J. (1975). *Animal Behaviour: An Evolutionary Approach.* Massachusetts, Sinauer Associations Incorporated. 547p.

ALDRICH, J.C. (1974). Allometric studies on energy relationships in the spider crab *Libinia emarginata* (Leach). *The Biological Bulletin 147*: 257-273.

ALDRICH, J.C. (1975a). Improved method for measurement of CO_2 in marine animals applied to 3 species of decapods. *Marine Biology 29(4)*: 277-282.

ALDRICH, J.C. (1975b). Oxygen consumption of crabs *Cancer pagurus* (L.) and *Maia squinado* (Herbst). *Comparative Biochemistry 50(A2)*: 223.

ALDRICH, J.C. (1975c). Individual variability in oxygen consumption rates of fed and starved *Cancer pagurus* and *Maia squinado*. *Comparative Biochemistry 51(A1)*: 175-183.

ALDRICH, J.C. (1976). The spider crab *Libinia emarginata* Leach, 1815 (Decapoda, Brachyura), and the starfish, an unsuitable predator but a co-operative prey. *Crustaceana 31(2)*: 151-156.

ALEXANDER, R.D. (1977). Natural selection and the analysis of human society. *In* Goulden, C.E. (Ed.) *Changing scenes in natural sciences 1776 - 1976*. Bicentennial Symposium Monograph, Philadelphia Academy of Natural Sciences 12: 283-377.

ALLEE, W.C. & DOUGLIS, M.D. (1945). A dominance order in the hermit crab *Pagurus longicarpus* Say. *Ecology 26*: 411-412.

ALLEN, J.A. (1966). The rhythms and population dynamics of decapod Crustacea. *Oceanography and Marine Biology 4*: 247-265.

ALLEN, J.A. (1972). Recent studies on the rhythms of post-larval decapod Crustacea. *Oceanography and Marine Biology Annual Review 10*: 415-436.

ALTMAN, J.S. (1967). The behaviour of *Octopus vulgaris* Lam. in its natural habitat: a pilot study. *Underwater Association of Malta, Underwater Association Report 1966-67*: 77-83.

ALTMANN, S.A. (1965). Sociobiology of rhesus monkeys. II. Stochastics of social communication. *Journal of Theoretical Biology 8*: 490-522.

ARNOLD, A.F. (1968). *The Sea Beach at Ebb-Tide*. Dover Publications Inc., New York. 490p.

ATKINSON, R.J. & NAYLOR, E. (1973). Activity rhythms in some burrowing decapods. *Helgoländer wiss. Meeresunters 24*: 192-201.

AURIVILLIUS, C.W.S. (1889). Die maskirung der Oxyrrhynchan Dekapoden, durch besondere anpassungen Ihres Körperbaues Vermittelt. *Kongl. Svenska Vetenskaps - Akademiens Handlingor 23(4)*: 1-71.

AUTRUM, H. & THOMAS, I. (1973). Comparative physiology of colour vision in animals. Pp. 661-692 *in* Jung, R. (Ed.) *Central Processing of Visual Information*. Handbook of Sensory Physiology VIII 3.

BAAL, H.J. (1953). Behaviour of spider crabs in the presence of octopuses. *Nature 171*: 887.

BAINBRIDGE, R. (1960). *Migrations*. Pp. 431-464 Waterman, T.H. Academic Press, London & New York.

BAKER, R.R. (1970). Bird predation as a selective pressure on the immature stages of the cabbage butterflies *Pieris rapae* and *P. brassicae*. *Journal of Zoology, London 162*: 43-59.

BANTOCK, C.R., BAYLEY, J.A. & HARVEY, P.H. (1976). Simultaneous selective predation on two features of a mixed sibling species population. *Evolution 29*: 636-649.

BARBER, S.B. (1961). Chemoreception and thermoreception. Pp. 109-132 *in* Waterman, T. (Ed.) *Physiology of Crustacea, Vol. II*. Academic Press, New York.

BARLOW, D.H., HERSEN, M., JACKSON, M. (1973). Single-case experimental designs. *Archives of General Psychiatry 29*: 319-325.

BARNES, H. (Ed.) (1964). *Oceanography and Marine Biology Annual Review, Vol. II.* George Allen & Unwin Ltd., London. 548p.

BARNETT, S.A. (1967). Attack and defense in animal societies. Pp. 35-56 *in* Clemente, C.D. & Lindsley, D.B. (Eds.) *Aggression and Defense: Neural Mechanisms and Social Patterns.* Proceedings from the Conference on Brain Function, 5th, UCLA. 361p.

BASIOLI, J. (1952). Rakovica *Maia squinado*. *Morsko ribarstvo 4*: 112-114.

BATESON, P.P.G. & KLOPFER, P.H. (1981). *Perspectives in Ethology, Vol. 4.* Plenum Press, New York. 249p.

BATESON, W. (1889-90). Notes on the senses and habitats of some Crustacea. *Journal of the Marine Biological Association 1*: 211-214.

BEER, C.G. (1959). Notes on the behaviour of two estuarine crab species. *Transactions of the Royal Society of New Zealand 86*: 197-203.

BENNETT, E.W. (1964). The marine fauna of New Zealand: Crustacea, Brachyura. *Bulletin New Zealand Department of Scientific and Industrial Research, 153.*

BENSON, W.W. (1972). Natural selection for Müllerian mimicry in *Heliconius erato* in Costa Rica. *Science, N.Y. 176*: 936-939.

BERRY, P.F. & HARTNOLL, R.G. (1970). Mating in captivity of the spider crab *Pleistacantha moseleyi* (Miers) (Decapoda, Majidae). *Crustaceana 19*: 214-215.

BETHE, A. (1897). Das Zentralnervensystem von *Carcinus maenas*. *Archiv für Mikroskopische Anatomie und Entwicklungsmechanik 51*: 382-456.

BLAXTER, J.H.S. (1970). Light: Fish. Pp. 213-285 *in* Kinne, O. (Ed.) *Marine Ecology Vol. I(1).*

BLEST, A.D. (1957). The evolution of protective displays in the Saturnioidea and Sphingidae (Lepidoptera). *Behaviour 11*: 257-309.

BLEST, A.D. (1963). Longevity, palatability and natural selection in five species of New World saturnid moths. *Nature 197*: 1183-1186.

BOSCHI, E.E. & SCELZO, M.A. (1968). Larval development of the spider crab *Libinia spinosa* H. Milne Edwards reared in the laboratory (Brachyura, Majidae). Pp. 170-180 *in* Brill, E.J. (Ed.) *Studies on Decapod Larval Development*. Crustaceana Supplement (Leiden) 2.

BOVBJERG, R.V. (1953). Dominance order in the crayfish *Orconectes virilis* (Hagen). *Physiological Zoology 26*: 173-178.

BOVBJERG, R.V. (1956). Some factors affecting aggressive behaviour in the crayfish. *Physiological Zoology 29(2)*: 127-136.

BOVBJERG, R.V. (1959). Density and dispersal in laboratory crayfish populations. *Ecology 40(3)*: 504-506.

BOVBJERG, R.V. (1960a). Behavioural ecology of the crab *Pachygrapsus crassipes*. *Ecology 41*: 668-672.

BOVBJERG, R.V. (1960b). Courtship behaviour of the lined shore crab *Pachygrapsus crassipes* Randall. *Pacific Science 14*: 421-422.

BOYCOTT, B.B. (1954). Learning in *Octopus vulgaris* and other cephalopods. *Pubblicazioni della Stazione Zoologica di Napoli 25*: 67-93.

BOYCOTT, B.B. (1965). Learning in the octopus. *In* Eisner, T. & Wilson, E.O. (Eds.) *Animal Behaviour Readings from Scientific American (1975)*. San Francisco Scientific American. 339p.

BOYCOTT, B.B., LETTVIN, J.Y., MATURANA, H.R. & WALL, P.D. (1965). Octopus optic responses. *Experimental Neurology 12*: 247-256.

BOYCOTT, B.B. & YOUNG, J.Z. (1956). Memories controlling attacks on food objects by *Octopus vulgaris* Lamarck. *Pubblicazioni della Stazione Zoologica di Napoli 27*: 232-249.

BOYLE, P.R. & KNOBLOCH, D. (1981). Hole boring of crustacean prey by the octopus *Eledone cirrhosa* (Mollusca, Cephalopoda). *Journal of Zoology, London 193*: 1-10.

BREDER, C.M. (1946). An analysis of the deceptive resemblances of fishes to plant parts, with critical remarks on protective colouration, mimicry and adaptation. *Bingham Oceanographic Collection Bulletin 10(2)*: 1-49.

BREGAZZI, P.K. & NAYLOR, E. (1972a). Locomotor activity rhythm of *Talitrus saltator* (Montagu) (Crustacea, Amphipoda). *Journal of Experimental Biology 57*: 375-391.

BREGAZZI, P.K. & NAYLOR, E. (1972b). Effects of low temperature upon locomotor activity rhythm of *Talitrus saltator* (Montagu) (Crustacea, Amphipoda). *Journal of Experimental Biology 57*: 393-399.

BROEKHUYSEN, G.J. (1936). On development, growth and distribution of *Carcinides maenas* (L.). *Archives Neerlandaises de Zoologie Leiden 2*: 257-399.

BROUGH, E.J. (1965). Some aspects of the behaviour of *Robsonella australis* (Hoyle). *Transactions of the Royal Society of New Zealand 6(2)*: 7-19.

BROWN, F.A. (1960). Physiological rhythms. P. 401-430 *in* Waterman, T.H. (Ed.) *Physiology of Crustacea.* Academic Press, New York.

BRUCE, J.R., COLMAN, J.S. & JONES, N.S. (1963). *The marine fauna of the Isle of Man and its surrounding seas.* 2nd edition. University of Liverpool, Liverpool.

BRUNO, M.S., MOTE, M.I. & GOLDSMITH, T.H. (1973). Spectral absorption and sensitivity measurements in single ommatidia of the green crab, *Carcinus*. *Journal of Comparative Physiology 82*: 151-163.

BULLOCK, T.H. & HORRIDGE, G.A. (1965). *Structure and function in the nervous systems of invertebrates.* W.H. Freeman & Co., San Francisco.

BURGI, A.E. (1968). Contribution à l'étude du comportement vis-à-vis d'objets etrangers ches les Majidae. *Vie et Milieu 19*: 215-305.

BUSTARD, H.R. (1969). Defensive behaviour and locomotion of the Pacific boa *Candoia aspera*, with a brief review of head concealment in snakes. *Herpetologia 25*: 164-170.

CALMAN, W.T. (1911). *The Life of Crustacea.* Methuen, London. 289p.

CAMERON, A.M. (1966). Some aspects of the behaviour of the soldier crab *Myctryus longicarpus*. *Pacific Science 20*: 224-234.

CARLISLE, D.B. (1957). On the hormonal inhibition of moulting in decapod Crustacea. II. The terminal anecdysis in crabs. *Journal of the Marine Biological Association U.K. 36*: 291-307.

CARRICK, R. (1936). Experiments to test the efficiency of protective adaptations in insects. *Transactions of the Royal Entomological Society of London 85(4)*: 131-139.

CARYL, P.G. (1979). Communication by agonistic displays: what can games theory contribute to ethology? *Behaviour 68*: 136-169.

CARYL, P.G. (1981). Escalated fighting and the war of nerves: games theory and animal combat. Pp. 199-224 *in* Bateson, P.P.G. & Klopfer, P.H. (Eds.) *Perspectives in Ethology, Vol. 4.* Plenum Press, New York.

CARYL, P.G. (1982). Animal signals: a reply to Hinde. *Animal Behaviour 30*: 240-244.

CASE, J. & GWILLIAM, G.F. (1963). Amino acid detection by marine invertebrates. *Proceedings of the 16th International Congress of Zoology 3*: 75.

di CESNOLA, A.P. (1904). Preliminary note on the protective value of colour in *Mantis religiosa*. *Biometrika 3*: 58-59.

di CESNOLA, A.P. (1907). A first study of natural selection in *Helix arbustorum* (Helicogena). *Biometrika 5*: 387-399.

CHRISTIANSEN, M.E. (1971). Larval development of *Hyas araneus* (Linnaeus) with and without antibiotics (Decapoda, Brachyura, Majidae). *Crustaceana 21*: 307-315.

CLARKE, C.A., DICKINSON, D.G.C. & SHEPPARD, P.M. (1963). Larval colour pattern in *Papilio demodocus*. *Evolution 17*: 130-137.

CLARKE, R.B. (1962). Balanced polymorphism and the diversity of species. Pp. 47-70 *in* Nichols, D. (Ed.) *Taxonomy and geography*. Systematics Association, Oxford.

CLEMENTE, C.D. & LINDSLEY, D.B. (1967). *Aggression and defense: neural mechanisms and social patterns*. Proceedings from the Conference on Brain Function, 5th, UCLA, Los Angeles. 361p.

CLUTTON-BROCK, T.H. & HARVEY, P.H. (1979). Comparison and adaptation. *Proceedings of the Zoological Society of London B 205*: 547-565.

COOMBS, R.F. (1972). Device for detecting and measuring activity of large marine crustaceans. *New Zealand Journal of Marine and Freshwater Research 6*: 194-205.

COHEN, M.J. & DIJKGRAAF, S. (1961). Mechanoreception. Pp. 65-108 *in* Waterman, T. (Ed.) *Physiology of Crustacea, Vol. II*. Academic Press, New York.

COLMAN, J.A. (1972). Food of the snapper *Chrysophrys auratus* (Forster), in the Hauraki Gulf, N.Z. *New Zealand Journal of Marine and Freshwater Research 6(3)*: 221-239.

CORMACK, R.M. (1968). The statistics of capture - re-capture methods. *Oceanography and Marine Biology Annual Review 6*: 455-506.

CORNER, E.D.S., KILVINGTON, C.C. & O'HARA, S.C.M. (1973). Qualitative studies on the metabolism of Napthalene in *Maia squinado* (Herbst). *Journal of Marine Biological Association U.K. 53*: 819-832.

COTT, H.B. (1940). *Adaptive colouration in animals*. Methuen & Co. Ltd., London. 508p.

COURCHESNE, E. & BARLOW, G.W. (1971). Effect of isolation on components of aggressive and other behaviour in the hermit crab *Pagurus samuelis*. *Zeitschrift für vergleichende Physiologie 75*: 32-48.

COWDRY, E.F. (1911). The colour changes of *Octopus vulgaris* Lamarck. *University of Toronto Series of Biology Studies 10*: 1-53.

CRANE, J. (1941). Crabs of the genus *Uca* from the west coast of Central America. *Zoologica N.Y. 26*: 145-207.

CRANE, J. (1957). Basic patterns of display in fiddler crabs (Ocypodidae, Genus *Uca*). *Zoologica 42*: 69-82.

CRANE, J. (1958). Aspects of social behaviour in fiddler crabs, with special reference to *Uca maracoani*. *Zoologica 43*: 113-130.

CROOK, J.H. (1963). The basis of flock organisation in birds. *In* Thorpe, W.H. & Zangull, O.L. (Eds.) *Current problems in animal behaviour*. Cambridge University Press, Cambridge. 424p.

CROZE, H. (1970). Searching image in carrion crows. *Zeitschrift für Tierpsychologie 5*: 1-85.

CULLEN, E. (1957). Adaptations in the Kittiwake to cliff-nesting. *Ibis 99*: 275-302.

CULLEN, J.M. (1966). Ritualization of animal activities in relation to phylogeny, speciation and ecology. *Philosophical Transactions of the Royal Society, London B 251*: 363-374.

CURIO, E.B. (1973). Towards a methodology of teleonomy. *Experentia 29*: 1045-1058.

CURIO, E.B. (1976). *The Ethology of Predation*. Springer-Verlag, Berlin.

CUTRESS, C., ROSS, D.M. & SUTTON, L. (1970). The association of *Calliactis tricolor* with its pagurid, calappid and majid partners in the Caribbean. *Canadian Journal of Zoology 48*: 371-376.

DAWKINS, R. (1976). *The Selfish Gene*. Oxford University Press, Oxford. 224p.

DAWKINS, R. & KREBS, J.R. (1978). Animal signals: information or manipulation? Pp. 282-309 *in* Krebs, J.R. & Davies, N.B. (Eds.) *Behavioural Ecology*. Sinauer Associations Incorporated, Massachusetts.

DELL, R.K. (1963). *Native Crabs.* A.H. & A.W. Reed, Wellington. 64p.

DICE, L.R. (1945). Minimum intensities of illumination under which owls can find dead prey by sight. *American Naturalist 79*: 385-416.

DICE, L.R. (1947). Effectiveness of selection by owls of deer-mice (*Peromyscus maniculatus*) which contrast in colour with their background. *Contributions from the laboratory of vertebrate biology, University of Michigan 34*: 1-20.

DILLY, N., NIXON, M. & PACKARD, A. (1964). Forces exerted by *Octopus vulgaris*. *Pubblicazioni della Stazione Zoologica di Napoli 34*: 86-97.

DINGLE, H. & CALDWELL, R.L. (1969). The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* (Crustacea: Stomatopoda). *Behaviour 33*: 115-136.

DIXON, G.Y. & DIXON, A.F. (1891). Report on the marine invertebrate fauna near Dublin. *Proceedings of the Royal Irish Academy, Series 3 II*: 19-33.

DOAK, W.T. (1972). *Fishes of the New Zealand Region.* Hodder & Stoughton, Auckland. 132p.

DOUGLIS, M.D. (1946a). Some evidences of a dominance-subordinance relationship among lobsters, *Homarus americanus*. *Anatomical Record 96:* 553.

DOUGLIS, M.D. (1946b). Interspecies relationships between certain crustaceans. *Anatomical Record 96*: 553-554.

EDMUNDS, M. (1972). Defensive behaviour in Ghanian praying mantids. *Zoological Journal of the Linnean Society 5*: 1-32.

EDMUNDS, M. (1974). *Defence in animals. A survey of anti-predator defences.* Longman, Essex. 357p.

EGUCHI, E. & WATERMAN, T.H. (1966). Fine structure patterns in crustacean rhabdome. *In* Bernhard, C.G. (Ed.) *Functional organization of the compound eye.* Pergamon Press, Oxford. 105p.

EIBL-EIBESFELDT, I. (1952). Nahrungserwerb und Beuteschema der Erdkrote (*Bufo bufo* L.). *Behaviour 4*: 1-36.

EIBL-EIBESFELDT, I. (1967). Ontogenetic and maturational studies of aggressive behaviour. Pp. 57-94 *in* Clemente, C.D. & Lindsley, D.B. (Eds.) *Aggression and defence: neural mechanisms and social patterns*. Proceedings from the Conference on Brain Functions, 5th, UCLA, Los Angeles.

EISNER, T. & WILSON, E.O. (1975). *Animal Behaviour Readings from Scientific American. San Francisco Scientific American.* 339p.

EMLEN, J.M. (1973). *Ecology: An evolutionary approach.* Addison, Wesley, London. 493p.

ESSER, A.H. (Ed.) (1971). *Behaviour and environment.* Plenum Press, New York.

EWER, R.F. (1966). Juvenile behaviour in the African ground squirrel *Xerus erythropus* (E. Geoff.). *Zeitschrift fur Tierpsychologie*

FERNANDEZ, H.R. (1973). Spectral sensitivity and visual pigment of the compound eye of the galatheid crab *Pleuroncodes planipes*. *Marine Biology 20*: 148-153.

FIELD, L.H. (1977). A description and experimental analysis of a stereotyped cheliped flexion behaviour in hermit crabs. *Behaviour 61(3, 4)*: 147-179.

FIELDER, D.R. (1965). A dominance order for shelter in the spiny lobster *Jasus lalandei* (H. Milne-Edwards). *Behaviour 24*: 236-245.

FIELDER, D.R. & FRENCH, G.L. (1970). An activity recorder for bottom living marine crustaceans. *Crustaceana 19*: 208-210.

FINGERMAN, M. & LAGO, A.D. (1957). Endogenous twenty-four hour rhythms of locomotor activity and oxygen consumption in the crawfish *Orconectes clypeatus*. *American Midland Naturalist 58*: 383-393.

FISHER, R.A. (1930). *The genetical theory of natural selection.* Clarendon Press, Oxford. 291p.

FLATTELY, F.W. & WALTON, C.L. (1922). *The Biology of the Sea-shore.* Sidgwick & Jackson Ltd., London. 336p.

FORD, E.B. (1975). *Ecological Genetics.* 4th Edition. Chapman & Hall Ltd., London. 442p.

FRANK, L.H. & MEYER, M.E. (1972). Activity as a function of salinity in two species of inter-tidal crabs, *Hemigrapsus oregonensis* and *Hemigrapsus nudus*. *Psychonomic Science 27*: 169-170.

FRIEDMANN, H. (1944). The natural-history background of camouflage. *Smithsonian Institute Report (1943)*: 259-274.

FUZESSERY, Z.M. & CHILDRESS, J.J. (1975). Comparative chemosensitivity to amino acids and their role in the feeding activity of bathypelagic and littoral crustaceans. *Biological Bulletin 149(3)*: 522-538.

GARSTANG, W. (1890). Foreign substances attached to crabs. *Nature 41*: 417-418.

GODDEN, D.H. (1972). The motor innervation of the leg musculature and motor output during thanatosis in the stick insect *Carausius morosus*. *British Journal of Comparative Physiology 80*: 201-225.

GODDEN, D.H. (1974). Physiological mechanism of catalepsy in the stick insect *Carausius morosus*. *British Journal of Comparative Physiology 89*: 251-274.

GODDEN, D. & GOLDSMITH, T.H. (1972). Photoinhibition of arousal in the stick insect *Carausius*. *Zeitschrift für vergleichende Physiologie 76*: 135-145.

GODFRIAUX, B.L. (1969). Food of the predatory demersal fish in Hauraki Gulf. I: food and feeding habits of snapper. *New Zealand Journal of Marine and Freshwater Research 3(4)*: 518-544.

GODFRIAUX, B.L. (1974). Feeding relationships between tarakihi and snapper in western Bay of Plenty, New Zealand. *New Zealand Journal of Marine and Freshwater Research 8(4)*: 589-609.

GEORGE, M.J. (1965). Mark-recovery experiments in crustaceana. *Symposium Crustacea, Marine Biological Association, India. Part IV*: 1284-1295.

GOLDSMITH, T. & FERNANDEZ, H. (1968). Comparative studies of crustacean spectral sensitivity. *Zeitschrift für vergleichende Physiologie 60*: 156-175.

GOULD, S.J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews 41*: 587-640.

GOULD, S.J. & LEWONTIN, R.C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society, London B 205*: 581-598.

GOULD, S.J. & VRBA, E. (1982). Exaptation - A missing term in the science of form. *Paleobiology 8(1)*: 4-15.

GRAEFFE, E. (1882). Ueber die bei den Oxyrhynchen vorkommende Maskierung. Società adriatica di Scienze naturali Bollentino, Trieste.

GRAHAM, D.H. (1938). Food of fishes of Otago Harbour and adjacent seas. *Transactions and Proceedings of the Royal Society of New Zealand 68*: 420-436.

GRAY, I.E. (1957). A comparative study of the gill area of crabs. *Biological Bulletin 112(1)*: 34-42.

GRAZIADEI, P. (1971). The nervous system of the arms. Pp. 45-63 *in* Young, J.Z. (Ed.) *The anatomy of the nervous system of* Octopus vulgaris. Clarendon Press, Oxford.

GRIFFIN, D.J.G. (1966). The marine fauna of New Zealand: Spider Crabs, Family Majidae (Crustacea, Brachyura). *New Zealand Department of Scientific and Industrial Research Bulletin 172*. Wellington. 112p.

GRIFFIN, D.J.G. (1970). *Eurynome orientalis* a majid spider crab (Crustacea, Brachyura) new to Australia and notes on *E. granulosa*. *Journal of the Royal Society of Western Australia 53(1)*: 7-8.

GRIFFIN, D.J.G. (1973). Revision of spider crabs of genus *Phalangipus* (Crustacea, Brachyura, Majidae). *Journal of Natural History 7*: 165-207.

GRIFFIN, D.J.G. (1974). Spider crabs (Crustacea, Brachyura, Majidae) from the International Indian Ocean Expedition 1963-64. *Smithsonian Contributions to Zoology 182*: 1-35.

GRIFFIN, D.J.G. (1976). Spider crabs of family Majidae (Crustacea, Brachyura) from Philippine Islands. *Journal of Natural History 10(2)*: 179-222.

GRIFFIN, D.J.G. & TRANTER, H.A. (1974). Spider crabs of the family Majidae (Crustacea, Decapoda, Brachyura) from the Red Sea. *Israel Journal of Zoology 23*: 162-198.

GUYSELMAN, J.B. (1957). Solar and lunar rhythms of locomotor activity in the crayfish *Cambarus virilis*. *Physiological Zoology 30*: 70-87.

HAIG, J. & WICKSTEN, M.K. (1975). First records and range extensions of crabs in Californian waters. *Bulletin of Southern Californian Academy of Science 74(3)*: 100-104.

HAGERMAN, L. (1970). Locomotory activity patterns of *Crangon vulgaris* (Fabricius) (Crustacea, Natantia). *Ophelia 8*: 255-266.

HAILMAN, J.P. (1976). Uses of the comparative study of behaviour. Pp. 181-189 *in* Masterton, R.B. *et al.* (Eds.) *Evolution, brain and behaviour: persistent problems*.

HAMASAKI, D.I. (1968a). The electroretinogram of the intact anaesthetised octopus. *Vision Research 8*: 247-258.

HAMASAKI, D.I. (1968b). The ERG-determined spectral sensitivity of the octopus. *Vision Research 8*: 1013-1024.

HAMILTON, W.J. (1963). Success story of the opossum. *Natural History 72*: 17-25.

HAND, C. (1975). Behaviour of some New Zealand sea anemones and their molluscan and crustacean hosts. *New Zealand Journal of Marine and Freshwater Research 9(4)*: 509-527.

HART, J.F.L. (1960). The larval development of British Columbia Brachyura. II. Majidae, subfamily Oregoniinae. *Canadian Journal of Zoology 38*: 539-546.

HARTNOLL, R.G. (1961). A re-examination of the spider crab *Eurynome* Leach from British waters. *Crustaceana 2*: 171-182.

HARTNOLL, R.G. (1963). The biology of Manx spider crabs. *Proceedings of the Zoological Society of London 141*: 423-496.

HARTNOLL, R.G. (1964). The zoeal stages of the spider crab *Microphrys bicornutus* (Latr.). *Annual Magazine Natural History, Ser. 13(7)*: 241-246.

HARTNOLL, R.G. (1965). The biology of spider crabs: a comparison of British and Jamaican species. *Crustaceana 9*: 1-16.

HARTNOLL, R.G. (1968). Mating in the Brachyura. *Crustaceana 16*: 161-181.

HARTNOLL, R.G. (1974). Variation in growth pattern between some secondary sexual characters in crabs (Decapoda, Brachyura). *Crustaceana 27(2)*: 131-136.

HARTNOLL, R.G. (1978). The determination of relative growth in Crustacea. *Crustaceana 34(3)*: 281-293.

HARTWICK, E.B. & THORARINSON, G. (1978). Der associates of the giant Pacific octopus *Octopus dofleini* (Wulker). *Ophelia 17(1)*: 163-166.

HAYS, D. & GOLDSMITH, T.H. (1969). Microspectrophotometry of the visual pigment of the spider crab *Libinia emarginata*. *Zeitschrift für vergleichende Physiologie 65*: 218-232.

HAZLETT, B.A. (1966). Factors affecting the aggressive behaviour of the hermit crab *Calcinus tibicen*. *Zeitschrift für Tierpsychologie 23*: 655-671.

HAZLETT, B.A. (1968a). Communicatory effect of body position in *Pagurus bernhardus* (L.) (Decapod, Anomura). *Crustaceana 14*: 210-214.

HAZLETT, B.A. (1968b). Size relationships and aggressive behaviour in the hermit crab *Clibanarius vittatus*. *Zeitschrift für Tierpsychologie 25*: 608-614.

HAZLETT, B.A. (1969). Further investigations of the cheliped presentation display in *Pagurus bernhardus* (Decapoda, Anomura). *Crustaceana 17*: 31-34.

HAZLETT, B.A. (1970). Tactile stimuli in the social behaviour of *Pagurus bernhardus* (Decapoda, Paguridae). *Behaviour 36(1)*: 20-48.

HAZLETT, B.A. (1972a). Responses to agonistic postures by the spider crab *Microphrys bicornutus*. *Marine Behaviour and Physiology 1(1)*: 85-99.

HAZLETT, B.A. (1972b). Stereotypy of agonistic movements in the spider crab *Microphrys bicornutus*. *Behaviour 42*: 270-278.

HAZLETT, B.A. (1972c). Stimulus characteristics of an agonistic display of the hermit crab *Calcinus tibicen*. *Animal Behaviour 20*: 101-107.

HAZLETT, B.A. (1972d). Ritualization in marine Crustacea. Pp. 97-125 *in* Winn, H.E. & Olla, B.L. (Eds.) *Behaviour of Marine Animals. Vol. I: Invertebrates*. Plenum Press, New York.

HAZLETT, B. (1975a). Agonistic behaviour of two sympatric species of xanthid crabs, *Leptodius floridanus* and *Hexapanopus angustifrons*. *Marine Behaviour and Physiology 4*: 107-119.

HAZLETT, B.A. (1975b). Individual distance in the hermit crabs *Clibanarius tricolor* and *Clibanarius antillensis*. *Behaviour 52*: 253-265.

HAZLETT, B.A. (1975c). Ethological analyses of reproductive behaviour in marine Crustacea. *Pubblicazioni della Stazione Zoologica di Napoli 39*: 677-695.

HAZLETT, B.A. & BOSSERT, W.H. (1966). Additional observations on the communication systems of hermit crabs. *Animal Behaviour 14*: 546-549.

HAZLETT, B.A. & ESTABROOK, G.F.(1974). Examination of agonistic behaviour by character analysis. I. The spider crab *Microphrys bicornutus*. *Behaviour 48*: 131-143.

HAZLETT, B. & RITTSCHOF, D. (1975). Daily movements and home range in *Mithrax spinosissimus* (Majidae, Decapoda). *Marine Behaviour and Physiology 3*: 101-118.

HAZLETT, B.A., RITTSHOF, D. & RUBENSTEIN, D. (1974). Behavioural biology of the crayfish *Orconectes virilis*. I. Home range. *American Midland Naturalist 92*: 301-320.

HINDE, R.A. (1970). *Animal Behaviour: a synthesis of ethology and comparative psychology*. 2nd Edition. McGraw-Hill, Tokyo. 876p.

HINDE, R.A. (1975). The concept of function. *In* Baerends, G.P., Beer, C. & Manning, A. (Eds.) *Function and evolution in behaviour*. Oxford.

HINDLEY, J.P.R. & PENN, J.W. (1975). Activity measurement of decapod crustaceans: a comparison of white and infrared photographic illumination. *Australian Journal of Marine Freshwater Research 26*: 281-285.

HINSCH, G.W. (1968). Reproductive behaviour in the spider crab *Libinia emarginata* (L.). *Biological Bulletin 135*: 273-278.

HINSCH, G.W. (1970). Some factors controlling reproduction in the spider crab, *Libinia emarginata*. *Biological Bulletin 139*: 410.

HINSCH, G.W. (1972). Some factors controlling reproduction in the spider crab, *Libinia emarginata*. *Biological Bulletin 143*: 358-366.

HINSCH, G.W. (1973). Effects of eyestalk ablation on Y-organ in spider crab *Libinia emarginata*. *American Zoologist 13(4)*: 1353.

HINSCH, G.W. & CONE, M.V. (1969). Ultrastructure observations of vitellogenesis in the spider crab *Libinia emarginata* (L.). *Journal of Cellular Biology 40(2)*: 336-342.

HINSCH, G.W. & WALKER, M.H. (1971a). Penetration of oocyte envelope by spermatozoa in spider crab. *Journal of Ultrastructure Research 35*: 86.

HINSCH, G.W. & WALKER, M.H. (1971b). Spermatophore formation in vas-deferens of spider crabs. *Biological Bulletin 141*: 373.

HINSCH, G.W. & WALKER, M.H. (1974). Vas-deferens of spider crab *Libinia emarginata*. *Journal of Morphology 143(1)*: 1.

HOBSON, E.S. (1968). Predatory behaviour of some shore fishes in the Gulf of California. *U.S. Fish & Wildlife Service Research Report 73*: 1-92.

HOLLING, C.S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society, Canada 45*: 1-60.

HOLMES, S.J. (1906). Death-feigning in Ranatra. *Journal of Comparative Neurology 16*: 200-216.

HONEGGER, H.W. (1973a). Rhythmic motor activity responses of the California fiddler crab *Uca crenulata* to artificial light conditions. *Marine Biology 18*: 19-31.

HONEGGER, H.W. (1973b). Rhythmic activity responses of the fiddler crab *Uca crenulata* to artificial tides and artificial light. *Marine Biology 21*: 196-202.

HORRIDGE, G.A. & SHEPHEARD, P.R.B. (1966). Perception of movement by the crab. *Nature 209*: 267-269.

HUMPHRIES, D.A. (1971). Erratic movement and a cataleptic posture in the escape behaviour of fleas. *Entomologists' Monthly Magazine 106*: 200-202.

HUNTINGFORD, F.A. (1976). The relationship between inter- and intra-specific aggression. *Animal Behaviour 24*: 485-497.

HUGHES, D.A. (1966). Behavioural and ecological investigations of the crab *Ocypode ceratophthalmus* (Crustacea: Ocypodidae). *Journal of Zoology 150*: 129-143.

HUXLEY, J. (1942). *Evolution, the modern synthesis*. Harper & Brothers, New York. 645p.

HUXLEY, J.S. (1942). Constant differential growth-ratios and their significance. *Nature 114*: 895-896.

ISLEY, F.B. (1938). Survival value of acridian protective coloration. *Ecology 19*: 370-389.

JACHOWSKI, R.L. (1974). Agonistic behaviour of the blue crab *Callinectus sapidus* Rathbun. *Behaviour 50*: 232-253.

JACKMAN, L.A.J. (1968). *Marine Aquaria.* David & Charles, London. 168p.

JACKSON, R.R. & POLLARD, S.D. (1982). The biology of *Dysdera crocata* (Araneae, Dycderidae). Intraspecific interactions. *Journal of Zoology, London.* In press.

JENSEN, K. (1972). On the agonistic behaviour of *Carcinus maenus* (L.) (Decapoda). *Ophelia 10*: 57-61.

JOHNSON, C. (1976). *Introduction to Natural Selection.* University Park Press, Maryland. 213p.

JOLL, L.M. (1976). Mating, egg-laying and hatching of *Octopus tetricus* (Mollusca: Cephalopoda) in the laboratory. *Marine Biology 36*: 327-333.

JONES, H.G. (1969). Spider crabs of the genus *Mithrax* from Barbados. *Zoologischer Anzieger 182(5/6)*: 379-383.

JUNG, R. (1973). Central processing of visual information. *Handbook of Sensory Physiology VII 3*: 661-692.

KAESTNER, A. (1967). *Invertebrate Zoology.* Vol. 3. John Wiley & Sons, New York.

KAMPA, E.M. (1955). Euphausiopsin, a new photosensitive pigment from the eyes of euphausiid crustaceans. *Nature 175*: 996-998.

KAMPA, E.M., ABBOT, B.C. & BODEN, B.P. (1963). Some aspects of vision in the lobster, *Homarus vulgaris*, in relation to the structure of its eye. *Journal of the Marine Biological Association, U.K. 39*: 227-238.

KANCIRUK, P. HERRNKIND, P. (1973). Preliminary investigations of the daily and seasonal locomotor activity rhythms of the spiny lobster *Panulirus argus*. *Marine Behaviour and Physiology 1*: 351-359.

KATOH, G., YAMANAKA, I, OUCHI, A. & OGATA, T. (1956). General aspects on trawl fisheries in the Japan Sea. *Bulletin of the Japanese Sea Regional Fisheries Research Laboratory (Niigata, Japan) 4*: 1-331.

KAUFMAN, D.W. (1971). *Effects of pelage and substrate coloration on predation of mice by owls*. Ph.D. dissertation, University of Georgia, Athens, Georgia, U.S.A.

KAUFMAN, D.W. (1973). Shrike prey selection: colour or conspicuousness. *Auk 90*: 204-206.

KAUFMAN, D.W. (1974). Differential predation on active and inactive prey by owls. *Auk 91*: 172-173.

KAYES, R.J. (1974). The daily activity pattern of *Octopus vulgaris* in a natural habitat. *Marine Behaviour and Physiology 2*: 337-343.

KENNEDY, D. & BRUNO, M.S. (1961). The spectral sensitivity of crayfish and lobster vision. *Journal of General Physiology 44*: 1089-1102.

KETTLEWELL, H.B.D. (1955a). Selection experiments on industrial melanism in the Lepidoptera. *Heredity 9*: 323-342.

KETTLEWELL, H.B.D. (1955b). Recognition of appropriate backgrounds by the pale and black phases of Lepidoptera. *Nature 175*: 943-944.

KETTLEWELL, H.B.D. (1956). Further selection experiments on industrial melanism in the Lepidoptera. *Heredity 10(3)*: 287-301.

KETTLEWELL, H.B.D. (1958). Industrial melanism in the Lepidoptera and its contribution to our knowledge of evolution. *Proceedings of the Tenth International Congress of Entomology 2*: 831-841.

KETTLEWELL, H.B.D. (1959). Brazilian insect adaptations. *Endeavour 18*: 200-210.

KETTLEWELL, H.B.D. (1961). Selection experiments on melanism in *Amathes glareosa* Esp. (Lepidoptera). *Heredity 16*: 415-434.

KINNE, O. (1970). *Marine Ecology*. Vol. I(1). Wiley, London.

KIRK, R.M. (1975). Coastal changes at Kaikoura, 1942-74 determined from air photographs. *New Zealand Journal of Geology and Geophysics 18(6)*: 787-801.

KLOPFER, P.H. & HATCH, J.J. (1968). Experimental considerations. Pp. 31-43 *in* Sebeok, T.A. (Ed.) *Animal Communication*. Indiana University Press, Bloomington.

KNUDSEN, J.W. (1964a). Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science 18*: 3-33.

KNUDSEN, J.W. (1964b). Observations of the mating process of the spider crab *Pugettia producta* (Majidae, Crustacea). *Southern California Academy of Sciences Bulletin 63*: 38-41.

KREBS, J.R. (1973). Behavioural aspects of predation. Pp. 73-111 *in* Bateson, P.P.G. & Klopfer, P.H. (Eds.) *Perspectives in Ethology, Vol. I.*

KREBS, J.R. & DAVIES, N.B. (1978). *Behavioural Ecology*. Sinauer Associations Incorporated, Massachusetts.

KREBS, J.R. & DAVIES, (1981). *An Introduction to Behavioural Ecology*. Blackwell Scientific Publications, Oxford. 292p.

KREBS, J.R., ERICHSEN, J.T., WEBBER, M.I. & CHARNOV, E.L. (1977). Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour 25*: 30-38.

LAGLER, K.F. (1949). *Studies in freshwater fishery biology*. Ann Arbor, Michigan.

LANE, F.W. (1960). *Kingdom of the Octopus*. Sheridan House, New York. 300p.

LEBOUR, M.V. (1927). Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity, with a description of the larval stages of *Inachus dorsettensis*, *Macropodia longirostris* and *Maia squinado*. *Journal of the Marine Biological Association of the United Kingdom 14*: 795-821.

LEBOUR, M.V. (1928). The larval stages of the Plymouth Brachyura. *Proceedings of the Zoological Society of London 1928*: 473-560.

LE SUEUR, R.F. (1953). Note on the behaviour of the common spider crab. *Bulletin de la Societie de Jersiaise 16*: 37-38.

LEYHAUSEN, P. (1971). Dominance and territoriality as complemented in mammalian social structure. *In* Esser, A.H. (Ed.) *Behaviour and Environment*. Plenum Press, New York.

LOCHHEAD, J.H. (1961). Locomotion. Pp. 313-364 *in* Waterman, T. (Ed.) *Physiology of Crustacea, Vol. II*. Academic Press, New York.

LOWE, M.E. (1956). Dominance-subordinance relationships in the crawfish, *Cambarellus shufeldtii*. *Tulane Studies in Zoology 4*: 139-170.

McBRIDE, G. (1971). Theories of animal spacing: the role of flight, fight and social distance. Pp. 53-68 *in* Esser, A.H. (Ed.) *Behaviour and Environment: the use of space by animals and man*. Plenum Press, New York.

McCULLOCH, A.R. (1925). Stonefishes and the art of camouflage. *Australian Museum Magazine 2*: 159-162.

MacGINITIE, G.E. & MacGINITIE, N. (1968). *Natural History of Marine Animals*. 2nd Edition. McGraw-Hill, New York. 523p.

McLAY, C.L. (1981). *A Glossary of Population Biology*. 2nd Edition. University of Canterbury, Christchurch, New Zealand. 238p.

McLEAN, R.B. & MARISCAL, R.N. (1973). Protection of a hermit crab by its symbiotic sea anemone *Calliactis tricolor*. *Experentia 29*: 128-130.

McLEESE, D.W. (1968). Temperature resistance of spider crab *Chionoectes opilio*. *Journal of the Fisheries Research Board of Canada 25(8)*: 1733-1736.

McLEESE, D.W. & WATSON, S. (1968). Oxygen consumption of spider crab (*Chionoectes opilio*) and the American lobster (*Homarus americanus*) at low temperatures. *Journal of the Fisheries Research Board of Canada 25(8)*: 1729-1732.

MALDONADO, H. (1964). The positive learning process in *Octopus vulgaris*. *Zeitschrift für vergleichende Physiologie 47*: 191-214.

MANLY, B.F.J., MILLER, P. & COOK, L.M. (1972). Analysis of a selective predation experiment. *American Naturalist 106*: 719-736.

MARISCAL, R.N. (Ed.) (1974). *Experimental Marine Biology*. Academic Press, New York. 373p.

MARLER, P.R. (1968). Visual systems. Pp. 103-126 *in* Sebeok, T.A. (Ed.) *Animal Communication*. Indiana University Press, Bloomington.

MASTERTON, R.B., HODOS, W. & JERISON, H. (1976). *Evolution, brain and behaviour: persistent problems*. Erlbaum, Hillsdale, New Jersey.

MAYNARD-SMITH, J. (1974). The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology 47*: 209-221.

MAYNARD-SMITH, J. & PRICE, G.R. (1973). The logic of animal conflict. *Nature 246*: 15-18.

MAYR, E. (1961). Cause and effect in biology. *Science 134*: 1501-1506.

MAYR, E. (1974). Teleological and teleonomic, a new analysis. *Boston Studies in the Philosophy of Science 14*: 91-117.

MESSENGER, J.B. (1968). The visual attack of the cuttlefish *Sepia officinalis*. *Animal Behaviour 16*: 342-357.

MESSENGER, J.B. (1977a). Prey-capture and learning in the cuttlefish *Sepia*. Pp. 347-376 *in* Nixon, M. & Messenger, J.B. (Eds.) *The biology of cephalopods*. Symposia of the Zoological Society of London, 38. Academic Press, London.

MESSENGER, J.B. (1977b). Evidence that *Octopus* is colour blind. *Journal of Experimental Biology 70*: 49-55.

MESSENGER, J.B., WILSON, A.P. & HEDGE, A. (1973). Some evidence for colour-blindness in octopus. *Journal of Experimental Biology 59(1)*: 77-94.

MILLER, R.J. (1975). Density of the commercial spider crab, *Chionoectes opilio*, and calibration of effective area fished per trap using bottom photography. *Journal of the Fisheries Research Board of Canada 32*: 761-768.

MILLIGAN, H.N. (1915). The habits of the four-horned spider-crab. *Zoologist Series 4, 19*: 248-252.

MINKIEWICZ, R. (1907). Analyse expérimentale de l'instinct de deguisement chez les Brachyures, Oxyrhynques (Note preliminaire). *Archives de Zoologie Expérimentale et Generale 7(4)*: 37-67.

MINKIEWICZ, R. (1909). The instinct of self-concealment and the choice of colours in Crustacea. *Report of the Board of Regents of the Smithsonian Institution*: 465-485.

MOELLER, H.W., BENNETT, B., COUGHLIN, S. & GETZ, D. (1972). Predator-prey relationships under luminous conditions. *Marine Behaviour and Physiology 1*: 257-260.

MOLENOCK, J. (1976). Agonistic interactions of the crab *Petrolisthes* (Crustacea, Anomura). *Zeitschrift für tierpsychologie 41*: 277-294.

MOYNIHAN, M. (1975). Conservatism of displays and comparable stereotyped patterns among cephalopods. *In* Baerends, G., Beer, C. and Manning, A. (Eds.) *Function and evolution in behaviour*. Clarendon Press, Oxford. 393p.

MUSICK, J.A. & McEACHRAN, J.D. (1972). Autumn and winter occurrence of decapod crustaceans in Chesapeake bight, U.S.A. *Crustaceana 22(2)*: 190-200.

NAYLOR, E. (1958). Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). *Journal of Experimental Biology 35(3)*: 602-610.

NAYLOR, E. (1960). Locomotory rhythms in *Carcinus maenas* (L.) from non-tidal conditions. *Journal of Experimental Biology 37*: 481-488.

NAYLOR, E. (1961). Spontaneous locomotor rhythm in Mediterranean *Carcinus*. *Pubblicazioni della Stazione Zoologica di Napoli 32*: 58-63.

NEILL, S.R. & CULLEN, J.M. (1974). Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *Journal of Zoology, London 172*: 549-569.

NICHOLS, D. (1962). *Taxonomy and Geography*. Systematics Association, Oxford.

NININGER, H.H. (1918). Crabs taken at Laguna beach in the summer of 1916. *Pomona College Journal of Entomology and Zoology 10(2)*: 36-42.

NISHIMURA, S. & MIZUSAWA, R. (1969). On the possible natural interbreeding between *Chionoectes opilio* (O. Fabricius) and *C. japonicus* Rathbun (Crustacea: Decapoda) a preliminary report. *Seto Rinkai jilkenjo Publication 17*: 193-205.

NIXON, M. & DILLY, P.N. (1977). Sucker surfaces and prey capture. *In* Nixon, M. & Messenger, J.B. (Eds.) *Biology of Cephalopods*. Zoological Society of London, 38. Academic Press, London. 615p.

NIXON, M. & MESSENGER, J.B. (1977). *The Biology of Cephalopods*. Zoological Society of London, 38. Academic Press, London. 615p.

NOLAN, B.A. & SALMON, M. (1970). The behaviour and ecology of snapping shrimp (Crustacea) *Alpheus heterochelis* and *Alpheus normanni*. *Forma et functio 2*: 289-335.

OOI, T.C. (1967). *The casemoth* Liothula omnivora *(Psychidae: Lepidoptera)*. M.Sc. Thesis, Massey University, Massey, New Zealand.

ORMOND, R.F.G., HANSCOMB, N.J. & BEACH, D.H. (1976). Food selection and learning in the crown-of-thorns starfish *Acanthaster planci*(L.). *Marine Behaviour and Physiology 4*: 93-105.

PACK, Y.M. (1975). *The effects of algal deprivation and chela amputation on the masking activities of the camouflage crab* Notomithrax ursus *(Oxrhyncha: Majidae)*. Unpubl. B.Sc. Honours thesis, University of Canterbury, Christchurch, New Zealand.

PACKARD, A. & SANDERS, G.D. (1969). What the octopus shows to the world. *Endeavour 28*: 92-99.

PARDI, L. & PAPI, F. (1961). Kinetic and tactic responses. Pp. 365-400 *in* Waterman, T. (Ed.) *Physiology of Crustacea, Vol. II.* Academic Press, New York.

PARK, O., ROBERTS, T.W. & HARRIS, S.J. (1941). Preliminary analysis of activity of the cave crayfish *Cambarus pellucidus*. *American Naturalist 75*: 154-171.

PEARSE, A.S. (1911). The influence of different colour environments on the behaviour of certain arthropods. *Journal of Animal Behaviour 1(2)*: 79-110.

PEREYRA, W.T. (1966). The bathymetric and seasonal distribution, and reproduction of adult Tanner crabs, *Chionoectes tanneri* Rathbun [Brachyura: Majidae], of the northern Oregon coast. *Deep Sea Research 13*: 1185-1205.

PEREYRA, W.T. (1968). Distribution of juvenile Tanner crabs *Chionoectes tanneri* Rathbun). Life history model and fisheries management. *Proceedings of the National Shellfisheries Association 58*: 66-70.

PEREZ, C. (1929). Charactères sexuels chez un crabe oxyrhynque (*Macropodia rostrata* L.). *Compte rendus de l'Academie des Sciences, Paris 188*: 91-93.

POPHAM, E.J. (1941). The variation in the colour of certain species of *Arctocorisa* (Hemiptera, Coroxidae) and its significance. *Proceedings of the Zoological Society of London, Series A, III*: 135-172.

POULTON, E.B. (1887). The experimental proof of the protective value of colour and markings in insects in reference to their vertebrate enemies. *Proceedings of the Zoological Society of London 1887*: 191-274.

POULTON, E.B. (1890). *The colours of animals: their meaning and use.* Kegar, Paul Trench, Trubner, London. 360p.

RASMUSSEN, E. (1973). Systematics and ecology of the Isefjord marine fauna. *Ophelia 11*: 1-495.

RATHBUN, M.J. (1925). The spider crabs of America. *Bulletin of the United States National Museum 129*: 1-613.

REESE, E.S. (1962). Submissive posture as an adaptation to aggressive behaviour in hermit crabs. *Zeitschrift für Tierpsychologie 19*: 645-651.

REESE, E.S. (1964). Ethology and marine zoology. Pp. 455-488 *in* Barnes, H. (Ed.) *Oceanography and Marine Biology Annual Review, Vol. II.*

REMMERT, H. (1969). Tageszeitliche Verzahnung der Aktivität verschiedener Organismen. *Oecologia 3(2)*: 214-226.

RHODES, J.M. (1963). Simultaneous discrimination in *Octopus*. *Pubblicazioni della Stazione Zoologica di Napoli 33*: 83-91.

RITCHIE, L.D. (Ed.) (1970). Fishing Industry Board southern spider crab (*Jacquinotia edwardsii* (Jacquinot, 1853)) survey - Auckland Islands and Campbell Island 30/1/70 - 23/2/70. *Fisheries Technical Report, N.Z. Marine Department 52*: 1-111.

ROBERTSON, T.B. (1904). On the "sham-death" reflex in spiders. *Journal of Physiology 31*: 410-417.

ROBINSON, M.H. (1968). The defensive behaviour of the stick insect *Oncotophasma martini* (Griffini) (Orthoptera: Phasmatidae). *Proceedings of the Royal Entomological Society of London (A) 43(10-12)*: 183-187.

ROBINSON, M.H. (1969). Defences against visually hunting predators. Pp. 225-259 *in* Dobzhansky, T.H., Hecht, M.K. & Steere, W.M.C. (Eds.) *Evolutionary Biology, Vol. 3.* North Holland, Amsterdam.

ROBINSON, M.H. (1973). Insect anti-predator adaptations and the behaviour of predatory primates. *Actas-4 Congreso Latinoamericano de Zoologia 2*: 811-836.

ROBINSON, M.H. & OLAZZARI, J. (1971). Units of behaviour and complex sequences in the predatory behaviour of *Argiope argentata* (Fabricius) (Araneae: Araneidae). *Smithsonian Contributions to Zoology No. 65, Washington.*

RODRIGUEZ, G. & NAYLOR, E. (1972). Behavioural rhythms in littoral prawns. *Journal of Marine Biological Association, U.K. 52*: 81-95.

ROFFE, T. (1975). Spectral perception in *Octopus:* a behavioural study. *Vision R-search 5*: 353-356.

ROOT, R.B. (1967). Niche exploitation pattern of the blue-grey gnatcatcher. *Ecological Monographs 37*: 317-350.

ROPER, D.S. (1975). *The distribution, growth and sexual differentiation of the spider crab* Leptomithrax longipes. Unpubl. Dip. Sci. thesis, University of Otago, Dunedin, New Zealand.

ROSS, D.M. (1971). Protection of hermit crabs (*Dardanus* spp.) from octopus by commensal sea anemones (*Calliactis* spp.). *Nature 230*: 401-402.

ROSS, D.M. & von BOLETZKY, S. (1979). The association between the pagurid *Dardanus arrosor* and the actinian *Calliactis parasitica.* Recovery of activity in "inactive" *D. arrosor* in the presence of cephalopods. *Marine Behaviour and Physiology 6*: 175-184.

RUBENSTEIN, D.I. & HAZLETT, B.A. (1974). Examination of the agonistic behaviour of the crayfish *Orconectes virilis* by character analysis. *Behaviour 50*: 193-216.

RUGGIERO, L.F., CHENEV, C.D. & KNOWLTON, F.F. (1979). Interacting prey characteristic effects on Kestrel predatory behaviour. *The American Naturalist 113(5)*: 749-757.

de RUITER, L. (1952). Some experiments on the camouflage of stick caterpillars. *Behaviour 4(3)*: 222-232.

de RUITER, L. (1956). Countershading in caterpillars. *Archives Néerlandaises de Zoologie 11*: 285-341.

RUSSELL, B.C. (1971). *Ecological relationships of rocky reef fishes of north-eastern New Zealand*. Unpubl. M.Sc. thesis, University of Auckland, Auckland, New Zealand.

RUSSELL-HUNTER, W.D. (1968). *A Biology of Lower Invertebrates*. Macmillan, New York. 181p.

RYAN, E.P. (1966). Pheromone: evidence in a decapod crustacean. *Science 151*: 340-341.

SANDIFER, P.A. & van ENGEL, W.A. (1971). Larval development of the spider crab *Libinia dubia* H. Milne Edwards (Brachyura, Majidae, Pisinae) reared in laboratory culture. *Chesapeake Science 12(1)*: 18-25.

SANDIFER, P.A. & van ENGEL, W.A. (1972). Larval stages of the spider crab *Anasimus latus* Rathbun 1894 (Brachyura, Majidae, Inachinae) obtained in the laboratory. *Crustaceana 23*: 141-151.

SAVAGE, T. (1971). Mating of the stone crab *Menippe mercenaria* (Say) (Decapoda, Brachyura). *Crustaceana 20*: 315-316.

SCHIFF, H. (1963). Dim light vision of *Squilla manthis* L. *American Journal of Physiology 205*: 927-940.

SCHLEGEL, C. (1911). Sur le developpement de *Maia squinado* Latr. *Compte Rendue de l'Academie des Sciences 153*: 480-482.

SCHMITT, W.L. (1968). *Crustaceans.* University of Michigan Press, U.S.A. 204p.

SCHOFFENIELS, E. (1970). Isosmotic intracellular regulation in *Maja squinado* Risso. and *Penaeus azetcus. Archives Internationales de Physiology et de Biochimie 78*: 461-466.

SCHÖNE, H. (1961). Complex behaviour. Pp. 465-520 *in* Waterman, T. (Ed.) *Physiology of Crustacea, Vol. II.* Academic Press, New York.

SCHÖNE, H. (1968). Agonistic and sexual display in aquatic and semi-terrestrial Brachyuran crabs. *American Zoologist 8*: 644-654.

SCOTT, J.P. (1968). Observation. Pp. 17-30 *in* Sebeok, T.A. (Ed.) *Animal Communication.* Indiana University Press, Bloomington.

SCOTT, J.P. & FREDERICSON, E. (1951). The causes of fighting in mice and rats. *Physiological Zoology 24*: 273-309.

SEBEOK, T.A. (1968). *Animal communication. Techniques of study and results of research.* Indiana University Press, Bloomington. 686p.

SEGAL, E. (1970). Light: Invertebrates. Pp. 159-211 *in* Kinne, O. (Ed.) *Marine Ecology, Vol. I(1).*

SHAW, M.E. (1928). A contribution to the study of relative growth of parts in *Inachus dorsettensis. Journal of Experimental Biology 6*: 145-160.

SHEPPARD, P.M. (1951). Fluctuations in the selective value of certain phenotypes in the polymorphic land snail, *Cepaea nemoralis* (L.). *Heredity 5*: 125-134.

SIDMAN, M. (1960). *Tactics of Scientific Research.* Basic Books Inc., Publishers, New York.

SINCLAIR, M.E. (1977). Agonistic behaviour of the stone crab, *Menippe mercenaria* (Say). *Animal Behaviour 25*: 193-207.

SLATER, P.J.B. (1973). Describing sequences of behaviour. Pp. 131-153 *in* Bateson, P.P.G. & Klopfer, P.H. (Eds.) *Perspectives in Ethology, Vol. I.* Plenum Press, London.

SMITH, W.J. (1968). Message-meaning analyses. Pp. 44-60 *in* Sebeok, T.A. (Ed.) *Animal Communication.* Indiana University Press, Bloomington.

SMITH, W.J. (1977). *The behaviour of communicating. An ethological approach.* Harvard University Press, Cambridge, Massachusetts. 545p.

SOKAL, R.R. & ROHLF, F.J. (1969). *Biometry. The principles and practice of statistics in biological research.* W.H. Freeman & Co., San Francisco. 776p.

SOLLBERGER, A. (1965). *Biological rhythm research.* Elsevier Publishing Co., New York. 461p.

SPOTTE, S.H. (1970). *Fish and invertebrate culture: water management in closed systems.* Wiley, New York.

STALIO, L. (1877). Catalogo metodics e destrittivo dei crostacei dell Adriatico. *Atti R. Istituto Veneto di Scienze letere edavti Venice Atti 5*: 1-350.

STEBBING, T.R.R. (1893). *A history of crustacea.* The International Scientific Series, New York.

STEIN, R.A. & MAGNUSON, J.J. (1976). Behavioural response of crayfish to a fish predator. *Ecology 57*: 751-761.

von STEINIGER, F. (1933). Die erscheinungen der katalepsie bei stabheuschrecken und wasserlaufern. *Zeitschrift für morphologie der tiere 26*: 591-708.

STEVCIC, Z. (1963). Contribution à la connaissance de la pêche de l'Araignée de mer (*Maja squinado* Herbst) en adriatique. *General Fisheries Council for the Mediterranean, Proceedings and technical papers 7*: 99-102.

STEVCIC, Z. (1967). A short outline of the biology of the spinous spider crab. *Bulletin Scientifique Conseil des Academies de la RSF de Yougoslavie Section A Sciences Naturelles technique et medicales 12*: 313-315.

STEVCIC, Z. (1968). Relations interspecifiques de l'Araignée de mer. *Commission internationale pour l'exploration scientifique de la Mer Mediterranée. Rapports et proces-verbaux des réunions 19(2)*: 147-149.

STEVCIC, Z. (1971). Laboratory observations on the aggregations of the spiny spider crab (*Maja squinado* Herbst). *Animal Behaviour 19*: 18-25.

STIEVE, H. (1960). Die spectrale Empfindlichkeitskurve des Auges von *Eupagurus bernhardus* L. *Zeitschrift für vergteichende Physiologie 43*: 518-525.

STREET, P. (1952). *Between the Tides*. U.L.P., London. 172p.

STREET, P. (1966). *The Crab and its Relatives*. Faber & Faber, London. 167p.

SUMNER, F.B. (1934). Does 'protective coloration' protect? - results of some experiments with fishes and birds. *Proceedings of National Academy of Sciences, Washington 20*: 559-564.

SUMNER, F.B. (1935a). Evidence for the protective value of changeable coloration in fishes. *American Naturalist 69*: 245-266.

SUMNER, F.B. (1935b). Studies of protective color change. III. Experiments with fishes both as predators and prey. *Proceedings of National Academy of Sciences, Washington 21*: 345-353.

SUTHERLAND, N.S. (1957a). Visual discrimination of orientation by *Octopus*. *British Journal of Psychology 48*: 55-71.

SUTHERLAND, N.S. (1957b). Visual discrimination of orientation and shape by *Octopus*. *Nature, London 179*: 11-13.

SUTHERLAND, N.S. (1958). Visual discrimination of orientation of rectangles by *Octopus vulgaris* Lamarck. *Journal of Comparative and Physiological Psychology 51*: 452-458.

SUTHERLAND, N.S. (1961). Discrimination of horizontal and vertical extents by *Octopus*. *Journal of Comparative and Physiological Psychology 54*: 43-48.

SUTHERLAND, N.S., MACKINTOSH, N.J. & MACKINTOSH, J. (1963). Simultaneous discrimination training of octopus and transfer of discrimination along a continuum. *Journal of Comparative and Physiological Psychology 56*: 150-156.

SUTHERLAND, N.S. & MUNTZ, W.R.A. (1959). Simultaneous discrimination training and preferred direction of motion in visual discrimination of shape in *Octopus vulgaris* Lamarck. *Pubblicazioni della Stazione Zoologica di Napoli 31*: 109-126.

SWARTZ, R.C. (1976). Agonistic and sexual behaviour of the xanthid crab, *Neopanope sayi*. *Chesapeake Science 17(1)*: 24-34.

TAKI, I. (1941). On keeping octopods in an aquarium for physiological experiments with remarks on some operative techniques. *Venus 10*: 140-156.

TAYLOR, P.B. & CHEN, L. (1969). The predator-prey relationship between the octopus (*Octopus bimaculatus*) and the California Scorpionfish (*Scorpaena guttata*). *Pacific Science 23*: 311-316.

TEISSIER, G. (1933). Étude de la croissance de quelques variants sexuels chez *Macropodia rostrata* L. *Bulletin Biologique de la France et de la Belgique 67*: 401-444.

TEISSIER, G. (1934). Differences sexuelles dans la croissance des appendices de *Maia squinado* (L.). *Societe de biologie Comptes-rendus, Paris 117*: 668-671.

TEISSIER, G. (1935). Croissance des variants sexuels chez *Maia squinado* L. *Roscoff France Station Biologique Travaux 13*: 93-130.

TEISSIER, G. (1955). Allométrie de taille et variabilité chez *Maia squinado*. *Archives de Zoologie Expérimentale et Générale 92*: 221-264.

TEISSIER, G. (1960). Relative growth. Pp. 537-560 *in* Waterman, T.H. (Ed.) *The Physiology of Crustacea, Vol. I.* Academic Press, New York and London.

TEYTAUD, A.R. (1971). The laboratory studies of sex recognition in the blue crab *Callinectes sapidus* Rathbun. *University of Miami Sea Grant Technical Bulletin No. 15.* 63p.

THOMAS, G. (1977). The influence of eating and rejecting prey items upon feeding and food searching behaviour in *Gasterosteus aculeatus* L. *Animal Behaviour 25*: 52-66.

THOMAS, R.F. & OPRESKO, L. (1973). Observations on *Octopus joubini* and four laboratory reared generations. *Nautilus 87(3)*: 61-65.

THORP, J.H. (1978). Agonistic behaviour in crayfish in relation to temperature and reproductive period. *Oecologia 36*: 273-280.

THORPE, W.H. & ZANGWILL, O.L. (Eds.) 1902. *Current Problems in Animal Behaviour.* Cambridge University Press, Cambridge. 424p.

TINBERGEN, L. (1960). The natural control of insects in pine-woods. I. Factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie, Leiden 13*: 265-343.

TINBERGEN, N. (1951). *The Study of Instinct.* Clarendon Press, Oxford.

TINBERGEN, N. (1959). Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour 15*: 1-70.

TINBERGEN, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie 20*: 410-433.

TINBERGEN, N. (1965). Behaviour and natural selection. Pp. 521-542 *in* Moore, J.A. (Ed.) *Ideas in Modern Biology.* Proceedings XVI International Zoology Congress, Washington.

TINBERGEN, N. (1967). Adaptive features of the black-headed gull *Larus ridibundus* L. *Proceedings XIV International Ornithological Congress*: 43-59.

TINBERGEN, N., BROEKHUYSEN, G.J., FEEKES, F., HOUGHTON, J.C.W., KRUUK, H. and SZULC, E. (1962). Egg shell removal by the black-headed gull, *Larus ridibundus* L.; a behaviour component of camouflage. *Behaviour 19*: 74-117.

TINBERGEN, N., IMPEKOVEN, M & FRANCK, D. (1967). An experiment on spacing-out as a defence against predation. *Behaviour 28*: 307-321.

TOWN, J.C. (1979). *Aspects of the biology of* Astrostole scabra *(Hutton, 1872)*. Unpubl. Ph.D. thesis, University of Canterbury, Christchurch, New Zealand.

TURNER, E.R.A. (1961). Survival values of different methods of camouflage as shown in a model population. *Proceedings of the Zoological Society, London 136*: 273-284.

VANNINI, M. & SARDINI, A. (1971). Aggressivity and dominance in river crab *Potamon fluviatile* (Herbst). *Monitore zoologico italiano, Firenze 5*: 173-213.

VAUGHN, J.C. (1971). Satellite DNA analysis in spider crab *Libinia emarginata*. *Biological Bulletin 141*: 405.

VERNET-CORNUBERT, G. (1957). Note preliminaire sur la transformation de la pince des males du crabe Oxyrhynque *Pisa tetraodon* (Pennant). *Comptes rendus de l'Academie des Sciences, Paris 244*: 1085-1087.

VERNET-CORNUBERT, G. (1958). Biologie generale de *Pisa tetraodon* (Pennant). *Bulletin de l'Institut Oceanographique (Monaco) 1113*: 1-52.

VERNET-CORNUBERT, G. (1960). Influence de l'ablation des pedoncules oculaires sur la mue, la ponte et les charactères sexuels externes, de *Pisa tetradon* Pennant. *Bulletin Institute Oceanography (Monaco) 1186*: 1-24.

VERRILL, A.E. (1908). Decapod Crustacea of Bermuda: I. Brachyura and Anomura. Their distribution, variations and habits. *Transactions of the Connecticut Academy of Arts and Sciences 13*: 299-474.

WALD, G. (1968). Single and multiple visual systems in arthropods. *Journal of General Physiology 51*: 125-156.

WALD, G. & BURG, S.P. (1957). The vitamin A of the lobster. *Journal of General Physiology 40*: 609-625.

WALD, G. & HUBBARD, R. (1957). Visual pigment of a decapod crustacean: the lobster. *Nature 180*: 278-280.

WALKER, J.J., LONGO, N. & BITTERMAN, M.E. (1970). The octopus in the laboratory. Handling, maintenance, training. *Behaviour Research Method and Instruments 2(1)*: 15-18.

WARNER, G.F. (1970). Behaviour of two species of grapsid crab during intraspecific encounters. *Behaviour 36*: 9-19.

WARNER, G.F. (1977). *The biology of crabs*. Paul Elek (Scientific Books) Ltd., London.

WATERMAN, T.H. (1961). *Physiology of Crustacea. Vol. I: Metabolism and Growth; Vol. II: Sense Organs, Integration and Behaviour*. Academic Press, New York and London. 681p.

WATERMAN, T.H. (1961). Light sensitivity and vision. Pp. 1-64 *in* Waterman, T.H. *The Physiology of Crustacea, Vol. II*. Academic Press, New York and London. 681p.

WATSON, J. (1970). Maturity, mating and egg laying in the spider crab, *Chionoectes opilio*. *Journal of the Fisheries Research Board of Canada 27*: 1607-1616.

WATSON, J. (1972). Mating behaviour in the spider crab, *Chionoectes opilio*. *Journal of the Fisheries Research Board of Canada 29(4)*: 447-449.

WEBBER, W.R. & WEAR, R.G. (1981). Life history studies on the New Zealand Brachyura. 5. Larvae of the family Majidae. *New Zealand Journal of Marine and Freshwater Research 15*: 331-383.

WELLS, M.J. (1958). Factors affecting reactions to *Mysis* by newly hatched *Sepia*. *Behaviour 13*: 96-112.

WELLS, M.J. (1962). *Brain and behaviour in cephalopods*. Heinemann, London. 171p.

WELLS, M.J. (1963). Taste by touch: some experiments with *Octopus*. *Journal of Experimental Biology 40*: 187-193.

WELLS, M.J. (1964). Detour experiments with octopuses. *Journal of Experimental Biology 41*: 621-642.

WELLS, M.J. (1978). *Octopus: Physiology and Behaviour of an Advanced Invertebrate*. Chapman & Hall Ltd., London. 417p.

WELLS, M.J. & WELLS, J. (1956). Tactile discrimination and behaviour of blind *Octopus*. *Pubblicazioni della Stazione Zoologica di Napoli 28*: 94-126.

WELLS, M.J. & WELLS, J. (1970). Observations on the feeding, growth rate and habits of newly settled *Octopus cyanea*. *Journal of Zoology 161*: 65-74.

WENNER, A.M. (1972). Sex ratio as a function of size in marine Crustacea. *American Naturalist 106*: 321-350.

WICKSTEN, M.K. (1975). The agile spider crabs. *Sea Frontiers 21(3)*: 149-152.

WICKSTEN, M.K. (1975). Observations on decorating behaviour following molting in *Loxorhynchus crispatus* Stimpson (Decapoda, Majidae). *Crustaceana 29(3)*: 315-316.

WICKSTEN, M.K. (1976). Studies on the hooked setae of *Hyas lyratus* (Brachyura: Majidae). *Syesis 9*: 367-368.

WICKSTEN, M.K. (1978). Attachment of decorating materials in *Loxorhynchus crispatus* (Brachyura, Majidae). *Transactions of the American Microscopical Society 97(2)*: 217-220.

WICKSTEN, M.K. (1979). Decorating behaviour in *Loxorhynchus crispatus* Stimpson and *Loxorhynchus grandis* Stimpson (Brachyura, Majidae). Pp. 37-46 *in* Brill, E.G. (Ed.) *Studies on Decapod Larval Development*. Crustaceana Supplement (Leiden) 2.

WICKSTEN, M.K. (1980). Decorator crabs. *Scientific American 242(2)*: 146-154.

WILLIAMS, G.C. (1966). *Adaptation and natural selection.* Princeton University Press, Princeton, New Jersey. 307p.

WILSON, D.P. (1935). *Life of the shore and shallow sea.* Ivor, Nicholson & Watson, London. 150p.

WILSON, E.O. (1975). *Sociobiology: The New Synthesis.* Harvard University Press, Cambridge, Massachusetts. 697p.

WILSON, E.O. & BOSSERT, W.H. (1971). *A primer of population biology.* Sinauer Associations Incorporated, Sunderland, Massachusetts. 192p.

WINGET, R.R., MAURER, D. & SEYMOUR, H. (1974). Occurrence, size composition and sex ratio of the rock crab, *Cancer irroratus* Say, and the spider crab, *Libinia emarginata* Leach, in Delaware Bay. *Journal of Natural History 8*: 199-205.

WODINSKY, J. (1971). Movement as a necessary stimulus of *Octopus* predation. *Nature 229*: 493-494.

WOLKEN, J.J. (1971). *Invertebrate photoreceptors: a comparative analysis.* Academic Press, New York and London. 179p.

WOOD, F.G. (1963). Observations on the behaviour of *Octopus*. *16th International Congress of Zoology 1*: 73.

WOODS, J. (1965). Octopus watching off Capri. *Animals 7*: 324-327.

WRIGHT, H.O. (1968). Visual displays in Brachyuran crabs: field and laboratory studies. *American Zoologist 8*: 655-665.

YANG, W.T. (1968). The zoeae, megalopa, and first crab of *Epialtus dilatatus* (Brachyura, Majidae) reared in the laboratory. Pp. 170-180 *in* Brill, E.J. (Ed.) *Studies on Decapod Larval Development.* Crustaceana Supplement (Leiden) 2.

YARNALL, J.L. (1969). Aspects of the behaviour of *Octopus cyanea* Gray. *Animal Behaviour 17*: 747-754.

YOSHIDA, H. (1941). On the reproduction of useful crabs in Northern Korea (II) Suisan Kenkyushi. *Journal of Fisheries Research, Tokyo 36(7)*: 116-123.

YOUNG, J.Z. (1956). Visual responses by octopus to crabs and other figures before and after training. *Journal of experimental Biology 33*: 709-729.

YOUNG, J.Z. (1971). *The anatomy of the nervous system of* Octopus vulgaris. Clarendon Press, Oxford.

YOUNG, W.M. (1929). Marine fauna of the Chatham Islands. *Transactions and Proceedings of the New Zealand Institute 60*: 136-166.

ZAHAVI, A. (1975). Mate selection - a selection for a handicap. *Journal of Theoretical Biology 53*: 205-214.

- - - -

Pers. comm.

McLAY, C.L. - Zoology Department, University of Canterbury, Christchurch, N.Z.

MARYAN, M.E. - Zoology Department, University of Canterbury, Christchurch, N.Z.

TOWN, J.C. - Zoology Department, University of Canterbury, Christchurch, N.Z.